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Oceanology: Biology of the Ocean

Volume 2. Biological Productivity of the Ocean

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U.S. DEPARTMENT OF COMMERCE
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January 1985

NOAA TECHNICAL MEMORANDUM NMFS-F/NEC

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(continued on inside back cover)

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Volume 2. Biological Productivity of the Ocean

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INTRODUCTION TO THE ENGLISH EDITION

Volume 2 of the Biological Productivity of the Ocean was published in 1977 in Russian by the Nauka Press in Moscow. The Editor-in-Chief of the Volume is Dr. M. E. Vinogradov, Deputy Director of the Shirshov Institute of Oceanology, USSR Academy of Sciences, Moscow. During a USSR-USA symposium on marine ecosystems in Tallin, Estonia, USSR, parts of the volume were discussed. Our Soviet hosts responded favorably to a request that the entire volume be made available in an English edition. The Office of International Fisheries of the National Marine Fisheries Service kindly provided us with a translation of the original Russian text. Following the initial translation the volume was forwarded to Dr. Vinogradov for review by each of the section authors. This English edition includes photocopies of figures from the Russian text. In several instances they are poorly reproduced. Also, a number of terms that represent literal translations of Russian terminology may not be familiar to the reader. However, rather than delay the production of the volume any further, we decided to move ahead with distribution in its present form so as to make available to a wider scientific audience the results of a synthesis of a considerable number of marine ecosystem studies by Soviet scientists not otherwise readily available in English.

The volume is divided into two parts. Part 1 deals with the Ecology of Marine Communities, including chapters on the ecological concepts, the structure and development of pelagic, benthic, and coral reef communities in different global regions and from several viewpoints, including the adaptive significance of schooling in the sea (Chapters I, II, and III). Primary and secondary production is discussed in Chapter IV. Part 1 concludes with a treatment of ecosystem models in Chapter V.

Part 2 focuses on Human Activity with a discussion on the potentials for increasing yields from fishery resources in Chapter I and the actual and potential impacts of pollution on marine ecosystems in Chapter II.

The Volume represents an extensive synthesis of Soviet literature dealing with marine ecosystems which is discussed in relation to contemporary ideas of marine ecologists in other countries. An extensive listing of references in Russian and in English that supports the syntheses is included.

We are indebted to our Soviet colleagues for the many hours spent reviewing and correcting the English version of their chapters. A special thanks is extended to Dr. M. E. Vinogradov for his willingness to see the project through to completion following considerable correspondence, including the mailings of chapters from various ports-of-call made by research vessels of the Academy of Sciences. We are also pleased to acknowledge the cooperation of the Soviet Copyright Agency, Moscow, for approving the translation and distribution of the English edition. The assistance of Ms. Jurate Micuta and Ms. Prudence Fox of the Office of International Fisheries, NMFS, Washington, for expediting the volume and Albert Peabody for providing the initial translation is gratefully acknowledged. Production of the volume would not have been possible without the editorial assistance of Ms. Jennie Dunnington who provided invaluable technical assistance in editing and many long hours typing the entire manuscript. We are also grateful to Ms. Elisabeth Keiffer of the University of Rhode Island for her fine editorial assistance.

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National Marine Fisheries Service Laboratory
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1. General Ecologic Concepts as Applied to Marine Communities. The Community as a Continuum. (K. N. Nesis)

The concept of the "biocenosis" was introduced by Möbius (1877). Möbius defined a biocenosis as a community of organisms inhabiting an individual area of the environment; the composition and quantitative relationships of the species of a community correspond to the mean of the extremes of the environmental conditions. The members of the biocenosis, according to Möbius, directly or indirectly depend on each other and mutually serve each other so that a self-regulating biologic equilibrium is formed, fluctuating about its mean position (Hesse, 1924). This definition emphasizes first of all the biologic interconnection and interdependence of the organisms of the community. This concept, introduced by Möbius, is firmly rooted in ecology.

The most important stage in the development of marine ecology was the introduction of a quantitative method of investigation of the benthos and bottom communities, connected with the name of Petersen (1911-1918). Petersen, however, had a quite different understanding of the word community than did Möbius. Communities, according to Petersen, were statistical units, regularly repeated groups of species encountered together, recognized (and named) after the most numerous and characteristic species which "struck the eye." The studies of Petersen were quite fruitful and stimulated extensive development of research in the area of quantitative accounting for the benthos (Zenkevich, 1947, 1963). The term "Petersen communities" has been firmly implanted in the ecologic literature.

However, at the same time, a Möbius concept of the community as a group of ecologically related organisms continued to exist and develop. The view of the community as a structure with such close and numerous internal connections that it could be likened to human society or even a superorganism developed. "Animal communities . . . are not mere assemblages of species living together, but form closely knit communities or societies comparable to our own," wrote one of the founders of modern ecology, C. Elton (1927, p. 5). Naturally, for the proponents of this view, the Petersen concept of the community was unacceptable. As a result of the extended discussions of the 1920s and 1930s, two concepts were developed in ecology, particularly in hydrobiology: communities of animals are statistical units, and communities are biologic units (Thorson, 1957). The views of the proponents of the biologic concept are well reflected by the words of D. N. Kashkarov: "The word biocenosis is constantly applied to widely varied groups of organisms, without the slightest attempt to understand the connections between them, to understand the internal relationships in the biocenosis. . . . In this sense hydrobiologists are great offenders. Any isolated accumulation of various organisms is immediately referred to as a biocenosis. . . . The result is a purely formal . . . and therefore fruitless description of phenomena" (1938, p. 271).

The concept of the biocenosis as a super-organism (Thienemann, 1925; Clements, Shelford, 1939; etc.) has been severely criticized. Particularly important has been the criticism from those who look upon a community as a continuum. The view of a community as a group of unrelated species, which react similarly to environmental conditions and are distributed along a gradient of environmental factors in accordance with the degree of tolerance of each species, agrees well with the concept of the community as a statistical unit, but is incompatible with the biologic concept of the community.

The development of the biologic concept of the community was greatly influenced by the development of such concepts as the trophic level, food chain and stages of succession (Elton, 1927, 1934; Kashkarov, 1938, 1945; and others). A new step on this path was the combination of the dynamic aspect of community (succession) with the views of V. I. Vernadsky concerning the biogeochemical role of living matter and the development of the trophodynamic concept of ecology on this basis (Lindeman, 1942). The trophodynamic aspect of the study of aquatic ecosystems developed rapidly, leading to the development of the theory of food chains (Riley, 1963a), the quantitative theory of biological productivity of the sea (Cushing, 1959a), the introduction to hydrobiology of cybernetic concepts (Margalef, 1956, 1968; Patten, 1959, 1966), and the development of mathematical models of aquatic ecosystems (Riley, 1963; Cushing, 1959a; Vinberg, Anisimov, 1966; Lyapunov, 1971; Menshutkin, 1971; Vinogradov et al., 1971; Odum, 1975, etc.).

The study of the structure of aquatic communities has also led to extremely important conclusions. It has been found that the composition and relations of species in a biocenosis is not unambigiously determined by the peculiarities and mosaic of external conditions (the biotope). The leading species of common benthic biocenoses are selected according to the principle of the least competitive interactions (Ivlev, 1954; Shorygin, 1955). If we rank the leading species of a biocenosis in order of mean biomasses, the neighboring species in the series thus produced will generally belong to different trophic groups (Turpaeva, 1949, 1957; A. P. Kuznetsov, 1960), and if they are in the same trophic group, they usually belong to different zoogeographic groups (Neyman, 1963a, 1967). This rule, first determined empirically and later confirmed with extensive factual materials, has provided an important confirmation of the value of the Petersen concept of benthic communities.

Thus, in marine biology, two different views on marine communities have developed; more precisely, two models of marine communities have been created. The first model, widely used in planktonology, is based on the trophodynamic aspect of an ecosystem ("the Lindeman approach"). It looks upon a community as a system of organisms at various trophic levels, related primarily by predator-prey relationships, i.e., "strong relationships"--by analogy with physical phenomena in the microcosm (MacArthur, 1972). This aspect of a community is the basis of many models of ecosystems, beginning with the classic approach of Lotka and Volterra and extending to quite modern works.

The second model, more widespread among researchers studying benthic fauna, concentrates attention on the organisms of a single trophic level and their interactions. For simplicity, it is assumed that migrating organisms are not included in the biocenosis (Thorson, 1957; and others). This means that predators which enter a given biocenosis only to feed are practically not studied. If we consider that most of the floor of the seas and oceans lies below the zone of habitation of producers, it can be stated that a typical benthic biocenosis is populated primarily by consumers of detritus.

The interrelationship of species in both models, naturally, is studied on the basis of the same primary postulates of ecologic science--Elton's theory of the ecologic niche and the law of competitive exclusion of Volterra and Gause. The stability of the "vertical" model requires maximization and stabilization of relationships between species, since these species are of different trophic levels, while stability of the "horizontal" model requires minimization of species relationships, i.e., the greatest possible separation of niches.

The most important processes in marine biology in recent years have been related to reconsideration of these traditional models of ecosystems. In planktonology, works have been extensively developed on the study of "nonpredatory" ecologic relationships, primarily the interrelationships between organisms mediated by external metabolites (Johnston, 1955; Lucas, 1955, 1965; Provasoli, 1958; and many others), developing in the study of the ecologic metabolism of the sea (Khaylov, 1971). It has become clear that exocrines and dissolved organic matter bind the producers, consumers, predators and reducers into a single network, which corresponds more closely to the actual picture of a community than a network based only on trophic relationships. The role of external metabolites is varied: They act as food (dissolved organic matter), sources of indispensable substances (vitamins, particularly B_{12}, trace elements, vital amino acids), as substances which suppress the growth of competing organisms, as signalling substances, etc. Consideration of this type of relationships between species can answer many curious questions in the ecology of marine communities. For example, the differing demand for external metabolites such as growth substances and vitamins, the capability of a species to grow with a lower concentration of these substances, may be one of the factors involved in specialization of species of phytoplankton and one explanation of the "plankton paradox" (Hutchinson, 1961)--the coexistence of phytoplankton species with similar demands for the primary biogenes, which should, therefore, be in acute competition. Furthermore, if any organism requires a vital substance which it cannot obtain from sea water, it will be forced to consume sufficient food to satisfy the demand for this substance (the Liebig minimum law). If the minimum quantity of food necessary to satisfy the demand for the limiting substance is significantly greater than that quantity of food necessary to satisfy the energy demands of the organism, it will be energetically favorable to the organism to convert the food only to the stage at which the radicals and active centers required by the organism are split off, and then to excrete the remainder in minimally converted form. The ecologic effectiveness of a population in this case will be significantly lower than the calculated effectiveness based on metabolic, growth and generative demands alone, and the excretions can serve as food for other animals, particularly for DOM consumers.

The view on the benthic biocenosis as a community of independent organisms, equally reacting to the abiotic conditions of the environment, has been significantly modified by the acknowledgment of the tremendous, decisive role of biologic, or more precisely symphsiologic (V. N. Beklemishev, 1951) interrelationships in marine communities (reviews: Miloslavskaya, 1961, 1964). Minimization of the competitive interrelationships between species is a statistical, climactic aspect of the community; in the dynamic, successional aspect, we see the entire variety of inter- and intra-species interrelationships: when competition between two (or more) species modifies the reaction of these species to abiotic conditions, when the relationships of two (or more) species are modified by the influence of a third, etc. For example. the acorn barnacles *Chthamalus stellatus* can flourish throughout the entire intertidal area, but cannot withstand the competition of *Balanus balanoides*. As a result, they form a belt in the uppermost shore horizon, where the *Balanuses* cannot exist due to the severe environmental conditions. For the *Balanuses*, as for the *Chthamaluses*, the habitat conditions are better the lower the level at which they live. However, in the lower intertidal zone the dog-whelks *Nucella lapillus*, the principal enemy of the acorn barnacles, are numerous. Therefore, balanuses of all ages inhabit the upper level of the intertidal zone, while the lower level is inhabited only by large individuals, too large for *Nucella*. The existence of these three species is possible due to their varying tolerance to the stress conditions in the upper tidal levels, but their distribution in belts does not reflect the distribution of the optimal conditions for their existence at all (Connell, 1961a, b). The alga *Hedophyllum sessile* finds its optimal conditions of existence in the surf zone, but is numerous there only in areas with moderate wave action, since in heavy surf it cannot withstand the competition of *Laminaria setchelli* and *Lessoniopsis littoralis*. The sea urchins *Strongylocentrotus purpuratus* devour these algae and may consume them completely, thus liberating the place for *Hedophyllum*. If an area of the bottom is cleared from the sea urchins, then *Laminaria* and *Lessoniopsis* rapidly crowd out *Hedophyllum* and its associated algae (Dayton, 1975). Studies of this type of interrelationship between species have led to the development of the concept of "key species" in a biocenosis, the ecologic influence of which significantly exceeds their part in the number and biomass of the biocenosis. Usually, the key species is a predator, occupying a high position in the food pyramid of the biocenosis and consuming, selectively or nonselectively, organisms which, were it not for the restraining influence of the predator, could monopolize the space or food resources and thus squeeze out less competitive species. For example, the starfish Pisaster ochraceus feeds primarily on mussels. When these starfish are absent, the mussels are the masters of the tidal zone, squeezing out the balanuses and other animals and greatly reducing the species variety (Dayton, 1971; Fotheringham, 1974; Menge, 1972; Paine, 1966, 1969a, b, 1974). In exactly the same way, the starfish Pycnopodia helianthoides holds down the number of the urchins Strongylocentrotus spp.--macrophyte feeders (Mauzey and other, 1968). In the opinion of Payne (1966), the local species diversity is directly related to the effectiveness with which predators prevent monopolization of the primary necessary resources by a single dominant species. The number and biomass of such key predators are low--they also have a vulnerable link in their life cycle. This is usually so for the pelagic larvae or fry. In particular, one important limiting aspect in the life of the predator might be the heterogeneous and, consequently, unpredictable for the predator, distribution of the food on which the young animals feed (Birkeland, 1974).

The formation and existence of climax communities are possible only under stable environmental conditions, in which changes are predictable in terms of period, phase, and amplitude, and do not go beyond the limits of tolerance of the organisms. If the changes are sharp and unpredictable, the climax community is disintegrated or disrupted. The places which are liberated are occupied first by opportunistic species, characterized by rapid reproduction, early maturation, high fertility, short life cycle, high mortality, and simple population structure (Pianka, 1970, 1972). During the course of the succession, they are gradually replaced by more competitive dominant species. In permanently unstable biotopes, a climax is not established and opportunistic species predominate permanently. However, even in stable communities, they may exist, due to aperiodic (and therefore unpredictable) disruptions in the structure of the community, forcibly throwing it into the initial stages of succession. On the land, these disruptions are caused by forest fires, floods and other factors; at sea--by hurricanes, tsunamis, earthquakes, outbursts of predators, etc. Thus, during the past decade on the coral reefs of the Indo-West Pacific area (Great Barrier Reef, Guam, etc.), an unprecedented burst in the development of the "crown-of-thorn" starfish Acanthaster placi has been observed (Chesher, 1969; Pearson, Endean, 1969; and many others). The coral reefs of the Indo-West Pacific are among the most mature and stable of all ecosystems in shallow waters of the world ocean. Acanthaster is usually an extremely rare animal (a few individuals per square kilometer), with old individuals predominating in the population. The mature starfish feed exclusively on hermatypic corals, and the substances excreted as the starfish feed on the coral attract other starfishes. In cases of massive multiplication, this property may lead to the formation of accumulations of many starfish in small areas of reef damage, frequently hundreds of individuals. The starfish attack the coral and destroy it almost completely, and all of the fauna associated with the living coral die. On the surface of the dead coral, algae develop immediately, followed by soft corals, etc. This same succession is observed during restoration of a reef destroyed by an earthquake (D. V. Naumov, personal communication). Complete restoration of the disrupted community requires many years or even decades. It is not yet clear whether massive development of *Acanthaster* occurs periodically, or whether this is an unprecedented phenomenon, related to anthropogenic influence on the community (Endean, 1973). This sort of disruption of a mature community plays a significant role in the evolution of the reefs, creating a temporary mosaic of various stages of succession and allowing the existence of opportunistic and fugitive species (Grassle, 1973).

Human activity has the same sort of influence on a community. Opportunistic species occupy the primary position in the list of organisms indicating pollution. They are the last to disappear when pollution becomes fatal for all life, and the first to appear in the course of self-purification (Grassle, Grassle, 1974). Man's influence may also cause brief disruption of mature communities. For example, on the shores of Puget Sound (Washington), the climax community consists of ubiquitous colonies of mussels. During stormy weather, the mussels die due to the impacts of logs lost in timber floatage, which strike the rocks quite forcefully. The empty spaces thus formed are rapidly covered with a bacterial-algal film, after which these spots are inhabited by *Chthalamus dalli*, followed by *Balanus glandula*, then *B. cariosus* and finally young mussels which, with time, completely displace the algae, as well as the limpets, which feed on them, barnacles, etc. (Dayton, 1971; Payne, 1974).

The activity of "key species" can come to the same process--preventing full colonization of a space and of all available food resources by dominant species and exclusion of opportunistic species, except that they do this constantly and gradually, not catastrophically rapidly.

Studies of such processes have established the extremely important role of the indirect, "weak" (MacArthur, 1972) relationships between species, which may change the tolerance of species to abiotic and biotic environmental factors and shift the equilibrium of the direct relationships (Turpaeva, 1969, 1972; Turpaeva, Maksimov, 1971; Darnell, 1970; Dayton, 1971; and others).

The idea of the selection of communities from species which interact minimally with each other has been applied in works dedicated to the analysis of the structure of plankton ecosystems. In studying the phytoplankton of Pamlico Sound (North Carolina), Hulburt and Horton (1973) stated the hypothesis that conditions favoring the creation of a high biomass of phytoplankton might be dual: In one case, the growth of phytoplankton as a whole is accelerated, while in another, the interactions between species are minimized. In this latter case, one might observe either a stop in the growth of one species, allowing rapid multiplication of another, usually competing, species, or both species, multiplying rapidly and simultaneously, no longer hindering each other or, finally, the development of one species begins after the other, but their maxima overlap. The conditions of minimization of interaction, therefore, are manifested in that the influence of the law of competitive exclusion of species occupying the same niche, limiting the growth of the biomass, is removed; the "either-or" principle (either one species or another with which it competes) is replaced by the "and" principle.

However, in plankton communities, the possibility of dispersion of species into different ecological niches is in principle less than in benthic communities. Divergence as to type of substrate, of course, is impossible, as to synusia--quite difficult; the basis of specialization becomes differentiation as to the nature of food, time and conditions of feeding and seasons of development. Therefore, in plankton communities, the significance of weak interactions and the factors minimizing the interrelationships are probably significantly less important than in benthic communities.

In recent times, since the development of the modern concept of the biological niche--the "Hutchinson niche" (Hutchinson, 1957, 1959), the concept of stability of ecosystems and the relation of stability to processes of succession (MacArthur, 1955; Margalef, 1963a, b, 1968), the concept of packing density of niches (MacArthur, 1960, 1965) and the creation of the "stability-time" hypothesis (Sanders, 1968, 1969; Slobodkin, Sanders, 1969; Grassle, Sanders, 1973), it has become possible to consider two seemingly mutually exclusive concepts of the biocenosis--the statistical and biological ones--as two sides of a single coin. It can be thought that the biologic concept of the biocenosis analyzes the dynamics of the process of development of the architectonics (structure) of the community, while the statistical concept studies the result of this process, i.e., the structure of the climax community. In discussing the question of the structure of a community, we silently assume that the very concept "community = biocenosis" is unambiguously understood and reflects the actual natural phenomenon. However, this is far from completely accepted.

First of all, the concept of the community as an undivided unity of plant and animal organisms is widespread in ecology (V. N. Beklemishev, 1928; Kashkarov, 1933), as is the concept of the biocenosis as a union of organisms capable of independent existence (Allee and others, 1949). Many authors use the term biocenosis to refer only to a self-sustaining, energetically autonomous "large community," including producers, consumers and reducers (see Zaïka, 1967). From this standpoint, the Möbius biocenosis is not a biocenosis at all, but only a dependent or incomplete community; the population of an oyster bank, for which the term was first suggested, includes almost no producers and exists primarily on the organic matter (detritus) which is produced in other communities. If we strictly follow this point of view, we cannot apply the concept of the biocenosis to the benthos of zones below the lower boundary of the phytal area, in other words to the population of spaces covering more than 2/3 of the surface of the Earth; this concept is then also inapplicable to the fauna of the bathypelagic and abyssopelagic zones, as well as the oligotrophic areas of the pelagic zones in the tropical oceans. In other words, if trophic completeness and functional independence are considered necessary characteristics of a biocenosis, we must state that there is but one biocenosis on Earth--the Geomeride. It seems more correct to consider a community in its initial Möbius significance as a set of living organisms within the limits of a homogeneous biotope. A biocenosis may include either organisms of all trophic levels, or only consumers.

The constancy of the composition of a community and the distinctness of the boundaries between neighboring communities existing in the environment, which has no such constancy or clear boundaries, is possible, as V. N. Beklemishev (1928) emphasizes, only if there is some internal organizational factor, due to which certain combinations of organisms are stable, while those intermediate between them are unstable, even if they live under intermediate conditions. The existence of such a factor, however, is hardly axiomatic. There is another point of view, first stated in 1910 by the geobotanist L. G. Ramensky: Vegetation is a continuous whole. The species are autonomous and have no organic relationship with each other. Species which respond in the same way to certain environmental conditions inhabit the same area, but, due to the ecologic individuality of each species, the boundaries of the ranges of various species do not coincide, so that the groups of species merge smoothly with each other. There are no communities; there are only coinciding species within the limits of the continuum. This concept has become widespread in geobotanics since the late 1920s, and has extended into marine biocenology.

The concept of the marine benthic community as a continuum has been developed primarily by A. Lindroth (1935, 1973). In his opinion, the concepts of trophic levels and trophic connections should be applied not so much to individual species as to life forms. The distribution of species in communities depends primarily not on species-specific relationships between them, but rather on their relationships to environmental factors which they all encounter. A sharp gradient in the environmental factors represents a boundary for the extension of many species in the community simultaneously. If the gradient is not great, the species are distributed along the gradient independently of each other, so that a continual distribution develops. The boundaries of a community are not clearly outlined, communities merging one into another. The boundary of distribution of the ecologically dominant species is, naturally, the boundary for the fauna and flora associated with it as well. Lindroth (1973) suggests that homogeneous communities be called *coenotypes*, that communities with gradually changing composition be called *coenoclines*. Among the coenotypes, he distinguishes *abiogenic coenotypes*, limited by sharp gradients in abiotic conditions; *biogenic coenotypes*, related to changes in ecologic dominants; and *plateau coenotypes*, homogeneous communities with unclear clinal-type boundaries.

A typical example of a coenocline, according to Lindroth (1935), is the community of soft, silty bottoms. The composition of this community results from external factors. Definite and rather individualized communities may be encountered wherever a dominant species of organism develops, i.e., wherever the coenocline becomes a biogenic coenotype. In the opinion of Lindroth, based on the study of the benthos of Gullmar Fjord (western Sweden), it is quite impossible to distinguish associations for such regions, since the "colonies" gradually merge with each other, with no sharp boundaries. Many other researchers studying the benthos of soft bottoms have reached similar conclusions (Vorob'yev, 1949; Lie, 1968a, 1969, 1974; Lie, Kelley, 1970; Lie, Kisker, 1970).

A second example of an analogous structure of a community is to be found in the benthic communities of the intertidal and phytal zones. Boudouresque (1971a) demonstrated that the species composition of algae in the Mediterranean sea near Marseille changes continually with depth, the distribution of each species of algae changing along a transect independently of the others, although in some places there is a sudden change in species composition. A similar conclusion was reached by O. G. Kussakin et al. (1974, p. 23). At times, the fauna is distributed less discretely than the flora (Denisov, 1974; Boudouresque, 1971a, b). Of course, such cases--and the number of examples may be quite great--fit well into the system of Lindroth.

The empirical conclusions of Lindroth were subjected to theoretical analysis by Fager (1963), Mills (1969), G. F. Jones (1969), Boudouresque (1971a) and other authors (see the reviews of Longhurst, 1964, and W. Stephenson, 1973). It follows from these works that the species of animals and plants, both in the water, and on the bottom, are distributed so that each of them reacts to gradients of environmental factors independently of the others. The environmental factors may be abiotic or biotic, the latter including most commonly the influence of the dominant species, the edifier species. Communities of species are, strictly speaking, recurrent groups, i.e., groups of species which usually (in the statistical sense of the word) are encountered together. This simultaneous encountering of members of the group results from the similarity of their response to environmental factors. Under conditions of extreme variability of abiotic environmental factors, these factors may have a decisive influence on the composition of a community--such biotopes are occupied by "physically controlled communities." As the variability of the physical (abiotic) factors decreases, biotic relationships take over, and in biotopes with relatively stable abiotic conditions, "biologically accommodated" or "biologically fitted" communities arise. They differ from physically controlled communities in that the former are composed of species which react identically to certain gradients in abiotic conditions, while the latter consist of species which are "fitted" to each other, mutually adapted to coexistence. Thus, a community can be defined as a "group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups" (Mills, 1969, p. 1427). Each community is, therefore, a "relative continuum between relative discontinuities" (Boudouresque, 1971a, p. 132). To describe communities of this type, Boudouresque (1971b) used the concept of the nodum. A nodum is an accumulation ("constellation") of points in a certain hyperspace, completely or partially isolated from other such accumulations. Groups of species which react identically to environmental factors are nodes within the multidimensional continuum. A community is also a nodum, i.e., a sector of the continuum limited by a space of interrupted continuum, an ecotone. A biocenosis (parallel to a community in the sense of Thorson) is a nodum consisting of a certain number of elementary nodes--ecologic or recurrent groups.

It is not difficult to see that the concept of the community as a continuum limited by sectors of interrupted continuity corresponds best to the model of the biocenosis as a structure with negative interspecific correlations, i.e., with the least competitive interactions (Ivlev, 1954;

Shorygin, 1955; Turpaeva, 1949, 1957). Shorygin's "sharp-topped" biocenosis, i.e., a community with sharp domination of one species (or life form), will correspond in this case to the community of an edifier species or the biogenic coenotype of Lindroth,* while the "flat-topped biocenosis," without sharp domination of one species (or life form) will correspond to the abiogenic or plateau coenotype, i.e., a community of independent species.

The direct practical application of the concept just described is related to the identification of the boundaries of communities. This question has been greatly discussed in the literature (see Odum, 1975, Chapter 6, paragraph 3). It has been the practice of domestic specialists in the study of benthic fauna to make wide use of the principle of separation of biocenoses by the dominant (in biomass) species in a given sample or group of samples taken at the same or neighboring stations (Vorob'yev, 1949; Neyman, 1963a). If we accept the concept of the community as a continuum, it becomes impossible to distinguish communities on the basis of this characteristic. This would be impossible, even when the equipment usually used in expeditions for quantitative sampling could give us a completely adequate idea of the biomass of each species, which is not the case. At the present time, it is most frequently recommended that communities be differentiated by using the method of distinguishing recurrent groups (Fager, 1957, 1963; Fager, McGowan, 1963) and various variants of multidimensional analysis.

The initial question in the problem of the community as a continuum--the existence or nonexistence of an internal organizational factor--can now in principle be considered answered, since it has been demonstrated (Patten, 1961c, 1962, etc.) that the stability of a community of organisms is greater than the stability of their environment. Natural communities evolve, adapting their structure to the environmental conditions and optimizing their species composition and interspecific quantitative relationships. Maintenance of a stable structure of the community requires certain expenditures of energy, defined by the flow of negentropy (Patten, 1961a). The community reacts to environmental conditions in such a way as to create a structure allowing the greatest energy yield ("income") given the available distribution of resources. Therefore, communities which pay the lowest price (measured in units of negentropy) to maintain the corresponding structure receive a selective advantage (Patten, 1961b, 1963). Thus, certain states of communities of organisms are truly more stable than others, even with intermediate values of abiotic environmental factors.

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*In the limiting case, a biogenic coenotype consists of a community consisting of an edifier species and species directly related to it. This type of community is a consortium, which geobotanists define as a combination of dissimilar organisms closely related to a productive organism or population (core of the consortium) and with each other in their vital activity. An oyster bank is an example of a consortium.

The evolution of ecosystems as a process of increasing their degree of self-organization is now an established fact (Dunbar, 1960, 1972; Patten, 1966; Margalef, 1968). However, this does not negate the possibility of the existence of groups consisting of independent or weakly dependent species, which merge smoothly together. The evolution of communities may follow the path of increasing interconnections between organisms, or of minimizing interspecific relationships. In either case, however, the biocenotic levels of organization are less integrated, less individualized and less isolated than the organismic and population levels. As V. N. Beklemishev (1964) put it, the boundaries between communities are no less indefinite and difficult to see, but also no less real, than the boundaries between atmospheric or oceanic currents. From this it follows that the concept of the community as a continuum is quite applicable for analysis of a number of specific biocenotic situations and should take its place in the methodologic arsenal of marine biology.

2. The Spatial-Dynamic Aspect of Existence of Pelagic Communities

(M. E. Vinogradov)

Due to the mobility of the biotope, the water, pelagic communities differ significantly in their structural and functional characteristics from other marine communities, and the analysis of their development from this standpoint is of particular interest.

In the volume on "The Biologic Structure of the Ocean," in the chapters dedicated to the biogeography of pelagic animals and their distribution, it was stated that the bases of the areas of distribution of most species in the pelagic zone are related to quasi-steady circulation of the waters, usually including not only horizontal motion, but also vertical motion. The circulation may have various dimensions and various degrees of "openness." Sometimes, preservation in the circulation of but an insignificant portion of a population supports reproduction and the existence of the species with its area of distribution, even though most of the population is scattered and unproductively lost.

The great oceanic or shoreline circulations form the basis for the area of distribution of many planktonic species which, together with species transported from other circulating currents or entering a given circulation for a time as a result of vertical and horizontal (nektonic forms) migrations, make up the community of a given region.

The biotope of a community--the aquatic medium--is continually renewed, while its characteristics change regularly as a result of seasonal or hydrodynamic factors. The community populating the water also undergoes regular changes.

2.1 Communities in Cold-Water Regions

In regions with a clearly expressed seasonal cycle, changes are determined primarily by this cycle. They will be analyzed in greater detail in Chapter II, paragraphs 2-4; here, we will briefly discuss certain aspects, in order to show that the development of pelagic communities of cold-water and tropical regions of the ocean follows, on the whole, the same regularities.

In temperate and cold-water regions, the enrichment of the surface, euphotic layers with nutrient salts occurs primarily due to winter convection extending into the layer beneath the euphotic zone, where the concentration of nutrients is high throughout the year. The winter minimum in the development of phytoplankton is followed by the spring pulse, resulting from the increase in the intensity of solar radiation and, no less significantly, the development of stable stratification of the water above the basic pycnocline.

When the seasonal pycnocline develops, the bloom of phytoplankton may sometimes even begin beneath the ice (Konovalova, 1972), whereas in the spring, if insolation is sufficient, but stratification is not stable, the phytocenosis is subject to such great losses--transport of cells from the euphotic zone by turbulent mixing--that the avalanche-like bloom of phytoplankton does not occur.

Soon after the peak of the pulse, the phytoplankton begins to die, the water becomes rich in suspended and dissolved organic matter, which serves as the basis for the development of masses of bacteria and protozoa--the heterotrophic flagellata and infusoria (Sorokin, 1974; Pasternak, Shushkina, 1973). It is this "protonutriment" in the surface layers above the thermocline which serves as the food base for most of the herbivorous plankton, the quantity of which tends to increase rapidly, reaching its maximum 1-3 months after the beginning of the bloom. The biomass of the predators reaches its maximum later, and their pressure on the herbivorous plankton differs in different regions and, apparently, experiences significant annual fluctuations.

The developing community changes not only with time, but also, following the currents, moves in space. Since stratification (the development of the seasonal thermocline) may not occur simultaneously in different regions, even though they be close together, the communities in different areas in the moving water may be in different stages of maturity later on. However, these differences, even over large regions, are generally not great, so that the beginning of the spring pulse, over the great, hydrologically homogeneous areas of water, fluctuates within a narrow interval of time. The intensity of consumption of phytoplankton by zooplankton, even within the limits of a single zone or a single community, is also not uniform over the entire water area (Heynrih, 1957; Kashkin, 1962; Kamshilov et al., 1958; and others). As a result, the picture of distribution of plankton is always rather variegated in both the space and the seasonal respects.

2.2 Communities of the Tropical Regions

In the tropics, where seasonal cooling of the surface water is slight or nonexistent, winter convection does not occur. Enrichment of the surface layers with nutrients occurs primarily in areas of quasi-steady upwelling of water, caused by hydrodynamic factors (zones of divergence of currents, upwelling of water near the shores of continents, resulting from onshore winds, the influence of islands and underwater banks). Studies performed on special cruises of the VITYAZ have allowed us to construct a schematic diagram of the circulation of nutrients in the ecosystem of the active layer of the pelagic zone of the tropic ocean, which determines the picture of development of its community (Vinogradov et al., 1971).

In a zone where the water ascends, the pycnocline is close to the surface, nutrients penetrate into the surface layer, and development of phytoplankton begins in this layer. The water flows outward from the upwelling zone. Temperature (density) stratification of the layers of water becomes more precise, intermixing decreases and the upper boundary of the thermocline descends. Nevertheless, nutrients, as a result of turbulent intermixing, continue to reach the upper, mixed layer, from below, though in decreasing quantities (Fig. 1). This flux of nutrients from below is

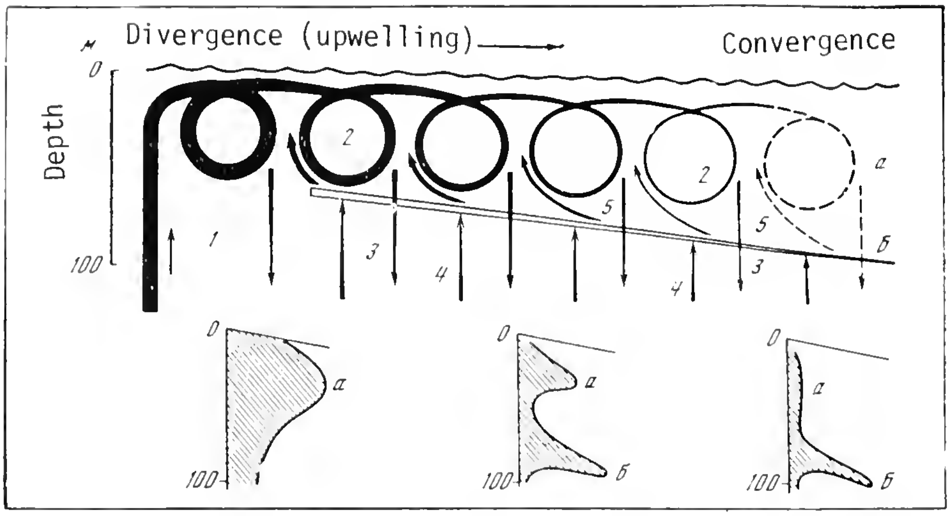

Fig. 1. Diagram of turnover of nutrients and dissolved organic matter (DOM) in the succession of a pelagic community in the tropic waters of the ocean. Top: 1, Ascent of nutrients and DOM in upwelling; 2, Repeated utilization in the cycle of production and destruction of the surface community; 3, Loss of nutrients with descending organic residue and migrating organisms; 4, Turbulent rising of nutrients and DOM and their retention at the lower maximum of phytoplankton and bacteria; 5, Intake of nutrients and DOM rising from the lower maximum layer into the productive cycle of the surface community. Bottom: Variation in distribution of relative quantity of phytoplankton at various distances from the upwelling zone (a, b, top and bottom phytoplankton maxima) (Vinogradov et al., 1971).

consumed by colonies of phytoplankton and bacteria formed in the layer above the thermocline, which serves as the dividing line between the portion of the community which lives above it and the source of nutrients below.

The population of the layers above the underlying maximum exists primarily on the nutrient salts transported by the flow of water from the ascending zone to the descending zone. These nutrients, entering the cycle of production and destruction of the community, are practically entirely contained in the bodies of organisms, their concentration in the water itself being close to analytic zero. The nutrient background of the surface layer decreases as the water "ages," due to the constant loss of a portion of the organic matter with the animals migrating into the depths and with the descending dying phytoplankton and detritus. As the community matures, it is carried with the water ever further from the location of the upwelling and, therefore, the time picture of development of the community is unrolled in space as well.

Since the upwelling of water occurs almost steadily, near the zone of water ascent the community is constantly in the initial stages of its development, with the maximum of phytoplankton,* while further downstream in the current we observe the maximum of herbivorous zooplankton, which requires more time for its development, and still further from the upwelling zone we find the maximum of predators (Vinogradov et al., 1961; Vinogradov, Voronina, 1964; Vinogradov et al., 1972; Timonin, 1971; Gueredrat, 1971). Consequently, the maxima of the biomass of the various groups, which require various lengths of time for their development, do not coincide in space (Chapter II, Fig. 3).

The spreading of zones of predominance of various trophic groups in space, accompanied by differences in number, biomass, dimensions and vertical distribution of plankton, allows us to look upon the individual stages in the development of the system as independent communities. Sometimes, this approach facilitates the study of the communities (Timonin, 1971; and others), since it allows us to ignore the degree of intermixing of the various communities with each other. However, obviously, we should always keep in mind that we are in fact analyzing and comparing not steady-state pictures, but rather individual frames from a continuous dynamic process.

The pelagic tropic communities require at least one or two months to achieve the comparatively mature state characteristic of the oligotrophic, halistatic areas in the central waters of the ocean. During this time, the community is carried by currents hundreds of miles from the region where it was formed by the upwelling of the water.

Actually, in the tropical ocean, the water of various streams of currents and the communities which it carries has significantly different "age." Therefore, there is a constant, more or less intensive, mixing of communities of varying degrees of maturity. Correspondingly, the picture of development of a community which we have studied, and for which quantitative mathematical models have been constructed (Vinogradov et al., 1972; Vinogradov et al., 1973) is rather idealized. In actual fact, the whole process is much more complex. First of all, the flow of water from the upwelling zone does not form an integral whole. At various depths, layers of water move at different speeds and in different directions. Secondly, the picture which we have presented of the "primary" succession in the ocean is rarely actually observed. It has been seen, for example, off the coast of Peru, near southwest Africa and in certain other regions of particularly intensive upwelling of water. Usually, however, the researcher

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*If the rise occurs at 10^{-3}-10^{-4} cm/s or somewhat greater, i.e., if the water rises by decimeters or meters per day, then a thermocline can form directly at the point where the water rises, and a phytoplankton bloom is observed. A bloom can develop in the rising water in three or four days (Smith et al., 1971; Strogonov, Vinogradov, 1975; and others). The more rapid the rise of the water, the closer to the surface the thermocline forms; if the rise is particularly rapid, for example, in the Peruvian upwelling, the water may rise tens of meters per day (Smith et al., 1971), the phytoplankton cannot reach its maximum development at the point where the water is rising, and the maximum is formed downstream from the point of the water ascent.

encounters a situation in which the waters rise from depths which are not very great, so that the waters which are rising are already populated by a developed community. In this case, the entire system, even in the zone of its formation, takes on a number of features which are characteristic of comparatively mature communities (Vinogradov, Semenova, 1975; Flint, 1975). Finally, changes in wind speed also cause changes in the rate of upwelling, while the axes of individual spots of upwelling of the water may be significantly deflected, leading to mechanical scattering of concentrations of zooplankton and phytoplankton at various depths (Strogonov, Vinogradov, 1975).

In spite of the fact that, under actual conditions, there is constant redistribution and mixing of communities, it is possible to observe communities in the early stage of maturity, and use them to obtain some idea of the basic regularities involved in succession changes. Obviously, in order to clarify the cause-and-effect dependence of phenomena and processes, we must study the entire picture of formation and development of the ecosystem. Isolated analysis of individual moments of its existence cannot allow us to understand either the causes of the observed state of the system, or its changes as time goes by.

2.3 The Succession of a Pelagic Ecosystem

The development of an ecosystem as time passes--its succession--is one of the fundamental concepts of modern ecology. In the opinion of Margalef (1968), succession in ecology occupies a position as important as that of evolution in general biology.

Succession is a process of self-organization, which occurs in any ecosystem. Margalef (1968) believes that any system consisting of reproducing and interacting organisms and the environment must continue to develop in the direction of creation of an organization for which the value of entropy per unit of information stored and transmitted is minimal. In the course of succession, structures (systems) are preserved which are most able to influence the future at the cost of the least amount of energy. In other words, the process of succession is equivalent to the process of accumulation of information. As it occurs, the system changes in the direction of achievement of a certain asymptotic steady state. In the initial stages, the community receives its primary influx of information from the surrounding (abiotic) environment, whereas in the more mature stages, the significance of information transmitted from some components of the community to others increases (Margalef, 1968).

This understanding of the succession changes in an ecosystem includes changes occurring in developing communities in the pelagic zone of the ocean. It is broader than the classical concept of succession, developed by continental geobotanists, which has caused some authors to express doubt as to the correctness of application of this term to the process of development of aquatic systems.

However, the differences between continental and oceanic systems are not differences of principle, but rather concern only certain of the peculiarities of the phenomena and their quantitative expression.

The essence of these differences is that aquatic, particularly pelagic, systems have a much greater degree of "openness," than do terrestrial systems. The great changes in the biotope in these systems occur primarily under the influence of abiotic factors, and they depend more than terrestrial systems on the arrival of nutrients from without. Furthermore, the concept of the final state (climax) in pelagic systems is less definite than in continental systems; however, this problem is less disturbing if we speak not of the climactic state of the system, but rather of its greater or lesser maturity.

It should be noted that the exploitation* of aquatic, particularly pelagic, systems, as a rule, is significantly higher than that of terrestrial systems. The extraction of organisms from the primary layer of habitation to depths unsuitable for their existence, the loss of organisms carried away by currents beyond the optimal area of habitation, the inroads of predators, all occur in pelagic systems with great intensity and encompass the overwhelming majority of the plankton population. The stronger exploitation, as is the case in terrestrial systems, retards or prevents the achievement of maturity by the system. From this point of view it is interesting that plankton systems reach relative maturity only in stratified water with weak intermixing, where the loss of phytoplankton cells from the euphotic zone is minimized.

One defining aspect of succession in the pelagic zone is the accumulation by the community of energy in the initial stages of its development and the preservation or expenditure of this store of energy in its more mature stages. Naturally, energy losses also occur in the early stages, energy accumulation in the more mature communities, but in the initial stages the processes of assimilation of energy, on the average, prevail over the processes of dissimilation, while, with the development of the community, this picture usually changes.

We emphasize once more that as pelagic zone ecosystems age and mature, changes occur not only in the biotic component--the community, but also in the biotope itself. First of all, the stratification of the layers of water becomes more stable, facilitating differentiation of the population and increasing the stability of the entire system.

What are the structural and functional changes which occur in a pelagic community as it matures? A summary of all available information on the succession of pelagic communities would occupy far too much space and is therefore not expedient, particularly if we consider that attempts have already been made in this direction (Margalef, 1958, 1962; Vinogradov et al., 1973; Gueredrat et al., 1972). Nevertheless, the primary trends in the changes should be analyzed.

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*"Exploitation" of a system refers to any removal of living organisms from the system (Margalef, 1968).

2.4 Changes in Structural Characteristics

The accumulation of information as the system matures leads, first of all, to an increase in the variety* in the community. However, it should be kept in mind that in mature communities, organisms which are taxonomically or trophically similar tend to form local accumulations, which decreases the variety encountered in small volumes of water. Nevertheless, the significance of variety for any individual is rather constant in various systems and increases as their maturity increases. Thus, for marine phytoplankton it varies from 1.4-2.0 bits (per individual) for young systems to 3.5-5.5 bits in later stages of succession (Zernova, 1974; Blasco, 1971). The upper limit of variety is not over 4.5-5.5 bits, which, possibly, is the limit of effectiveness in the construction of natural self-regulating systems.

The increase in variety which results from any ecologic succession or any process of self-organization of ecosystems touches the most varied characteristics of the community. For example, Margalef (1968, etc.) considers an increase in the variety of pigments to be a characteristic sign of the development of a phytoplankton community. However, the increase in variety is manifested most clearly as a change in the species composition of the community as it matures.

An increase in variety has been clearly demonstrated in the community of the tropical regions of the Indian Ocean (Timonin, 1971). In the regions of upwelling water--in the early stages of development of communities--the index of species variety of zooplankton was found to be 1.5-2 bits, while as the communities developed it increased to 2-2.5, and in comparatively mature communities in stable, stratified water, it reached 3.5-4 bits.

Simultaneously with species variety, trophic variety also increases (Fig. 2). In the early stages of succession, we find primarily nonspecialized herbivores or omnivores, while in the later stages, species with more selective feeding, consuming larger food items, predominate. The increase in the share of macrophages (predators) and the lengthening of the food chains are characteristic for mature oceanic systems (see Chapter II, paragraph 1).

The changes in the store of energy in a community are primarily manifested as changes in its biomass. In the initial stages of development, be it in spring in cold-water zones or in a region of quasistationary upwelling of water in the tropics, the biomass increases rapidly and is initially concentrated in the most labile link of the chain--the phytoplankton. At this time in the euphotic layer there is a store of nutrient substances, usually intensively replenished by the upwelling of the deeper water. In later stages, most of the nutrients of the system are concentrated

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*When speaking of variety, we should keep its spectrum in mind, since in individual small samples the variety of various systems may be identical, in spite of great differences in variety of the general sets involved.

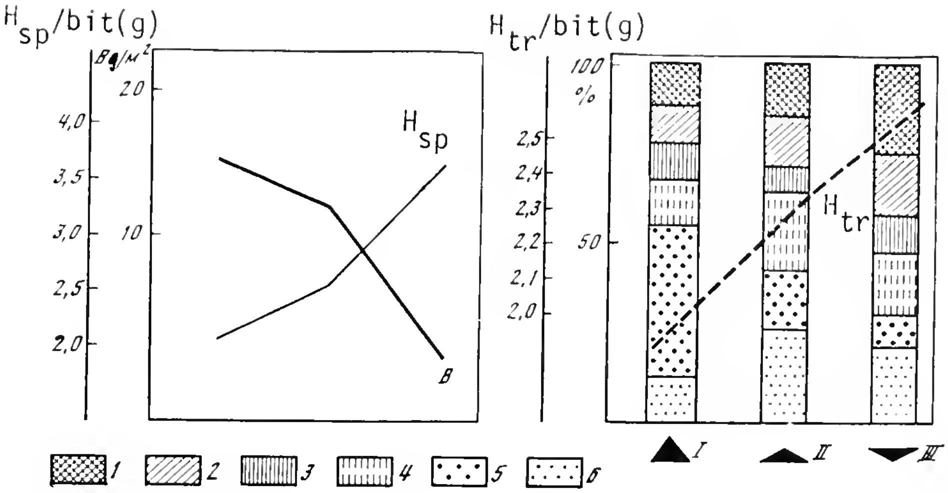

Fig. 2. Structural changes in the zooplankton communities with changes in the nature of vertical movement of the water (Timonin, 1971). I, Zone of intensive divergence; II, Intermediate zone, weak upwelling of water; III, Zone of convergence or stable stratification of water; B, Total biomass of zooplankton; H_{sp}, Species diversity; H_{tr}, Diversity in trophic structure; 1, Swallowing predators; 2, Biting predators; 3, Sucking predators; 4, Animals with mixed feeding (omnivores); 5, Coarse filter feeders; 6, Fine filter feeders.

in the bodies of its organisms. Soon, processes of dissimilation begin to predominate in the community and the total mass of plankton decreases. The maximum biomass, as the community develops, tends to shift along the trophic chain--first to the herbivores, then to the predaceous forms, leading to basic changes in the trophic structure of the community. The picture of displacement of the maximum of biomass upward along the trophic chain is clearly demonstrated by a model of the functioning of a tropical community (Vinogradov et al., 1971, 1973) (see Fig. 5.4) and by field observations (Vinogradov, Voronina, 1964; Tinomin, 1971; Gueredrat, 1971).

The increase in the mean dimensions of organisms as a community matures touches both phytoplankton and zooplankton. As the community matures, the significance of larger animals (macroplankton and micronekton) increases, while the mean dimensions of the animals of the mesoplankton and microplankton increase. For example, in the South Atlantic as we move from the South African upwelling to the central halistatic regions, the mean weight of microplanktonic and mesoplanktonic organisms increases by a factor of 3-3.5, while the fraction of mesozooplankton in nets and water bottle plankton from the upper 200 meter layer increases from 2/3 to 4/5 of the total mass of animals (Kovalev et al., 1976). As the biomass decreases and the mean dimensions of organisms increase, as we have seen, the variety of the community increases (see Fig. 2), i.e., these processes act as if they were inversely dependent (Sutcliffe, 1960; Longhurst, 1967; Timonin, 1971; etc.).

2.5 Changes in Functional Characteristics

The succession changes in biomass and trophic structure of communities are closely related to changes in their functional characteristics. The difficulties of quantitative evaluation of most of these usually force us to give only a qualitative estimate of many functional characteristics. However, the efforts expended in recent years in the study of pelagic ecosystems have in many cases allowed quantitative characterization of the succession changes in production not only for the lower trophic and ecologic groups (phytoplankton, bacteria), but also for higher levels and for the entire community as a whole, as well as estimation of the changes which occur in the course of succession in a number of other functional parameters: the degree of satisfaction of the demand for food (δ), the stress on trophic connections (ξ or κ), the degree of balance of production and consumption of various trophic levels (ε) and their ecologic effectiveness (ω).*

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*According to Slobdkin (1961), Menshutkin (1971), Vinogradov et al. (1976), $\delta = R_i/R_i^{max}$, where R_i is the actual ration, i.e., the food which an animal can consume given the available prey; R_i^{max} is the maximum ration, i.e., the quantity of food which the animal could consume to support its maximum growth rate.

$$\xi_j = \frac{\sum_i^n r_{ij}^{max} - P_j}{B_j},$$

where $\sum_i^n r_{ij}^{max}$ is the sum of the particular maximum rations of consumers, P_j is the production and B_j is the biomass of prey;

$$\kappa_j = \frac{\sum_i^n r_{ij}^{max}}{B_j}$$ is the index defining the pressure of predators on the biomass of a given prey species. These last two parameters show the extent to which, under the conditions present, organisms of the j^{th} group can be consumed and the extent to which the food requirements of consumers can be satisfied by the production of the prey;

$$\varepsilon_j = \frac{P_j}{\sum r_{ij}}$$ is the ratio of prey production to the sum total of the particular rations of predators, and shows the extent to which the production of a lower trophic level is utilized by organisms of the subsequent trophic levels;

As M. E. Vinogradov, E. A. Shushkina and I. V. Kukina (1976) have shown, in the early stages of development of a community with high biomass of autotrophs, the nutritional demands of the animals of all trophic levels are satisfied to a high extent ($\delta \simeq 0.8$), supporting an increase which is close to the maximum. As the community matures, the degree of satisfaction of the nutritional demands decreases ($\delta \simeq 0.4$-0.5). As δ decreases, the stress on the trophic connections between organisms at various trophic levels increases. The trophoecologic coefficient κ, showing the measure of pressure of consumers on the biomass of a given species, is less than 1 in the early stages of development of a community for practically all of its elements, whereas in more mature stages, particularly for the lower trophic levels, it increases rapidly.

On the basis of qualitative assumptions, it would seem probable that as a community matures, the degree of balance between production and consumption would increase. However, calculations show that the change in the degree of balance occurs quite differently at different trophic levels, and the assumption is valid only for some of them. Actually, the production of phytoplankton or bacteria may be underutilized, not only in the early stages of succession of the community but also, under certain conditions, in later stages, meaning that the general discussion of the degree of balance of production and consumption in communities of various stages of maturity and various trophic structure is not well founded.

The ecologic effectiveness of transmission of energy from one trophic level to another (ω) increases with increasing trophic level, and also as the community matures and the degree of satisfaction of nutritional demand decreases.

Calculations of change of the actual (P) and specific (P/B) production of various trophic levels of a community as it matures, performed for communities around the eastern Pacific equatorial upwelling (Sorokin et al., 1975a; b; Vinogradov et al., 1976) have shown that the production of the lower trophic levels (phytoplankton, bacteria, protozoa) decreases with maturation of the community more strongly than the production of mesoplankton, particularly predaceous forms. In certain groups (protozoa, predaceous mesoplankton) in a mature community the actual production may be negative, a result both of their increased consumption by other animals and of cannibalism within the group itself.

$\omega_{ij} = \frac{\sum_i r_{ij}}{R_j}$ is the index of the degree of utilization of the energy accumulated in a lower trophic level by the next higher trophic level.

The specific production of various elements of the community may also vary significantly as a function of the trophic relationships which develop in the community in various stages of its development. In general, as the community matures, the specific production of certain of its elements decreases, and in certain cases becomes negative (Vinogradov et al., 1976) (Fig. 3).

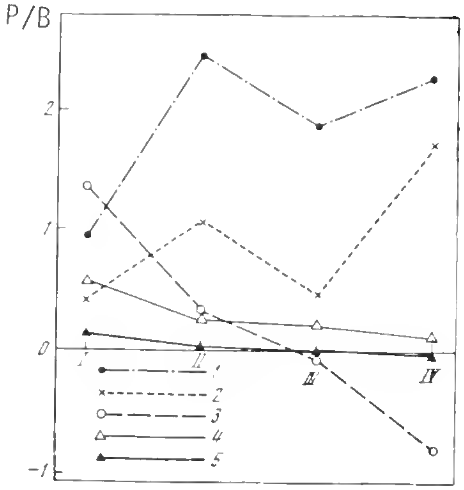

Fig. 3. Change in daily specific production (P/B) of various elements of a plankton community as upwelling weakens at the equator in the eastern Pacific (Vinogradov et al., 1976). 1, Phytoplankton; 2, Bacteria; 3, Protozoa; 4, Herbivores and Omnivores; 5, Carnivores; I, 97°W; II, 122°W; III, 140°W, IV, 153°W.

The actual and specific production of a zoocenosis and of an entire community are comparatively high in the early stages of development of the community, then decrease sharply or even become negative in the more mature stages, as dissipation of energy begins to occur in the community (Table 1).

All of the above leads us to the realization of the magnitude of the structural and functional changes experienced by a pelagic community as it grows and moves together with the water. Obviously, as we compare the ecosystems of various localities within a single large region, we should always keep in mind possible age differences of the communities, which may be responsible for many of the differences observed. Only a dynamic, succession approach to the study of ecosystems allows us to understand the causal dependence of the processes occurring within them.

Table 1. Production rates (P) of functional groups within the equatorial plankton ecosystem in 0-150 m layer in the eastern Pacific, k/cal m^{-2} day^{-1} (after Vinogradov et al., 1976 with corrections).

Stage of development of community	Phytoplankton	Bacteria	Protozoans	Metazoans		Entire community	
				herbivores	carnivores	P	P/B
Early (97°W)	24,1	6,6	1,9	2,8	1,0	5,9	0,12
More mature (140°W)	4,5	2,3	0,89	1,0	0,33	-3,2	-0,25

3. Nontrophic Regulatory Interactions of Marine Invertebrates.
(E. A. Zelickman)

3.1 Metabolic Regulation

Chemical communication is the most ancient of all systems of exchange of information between organisms and, correspondingly, of regulation of intrapolation and intraspecific relationships. The chemical substances excreted by plants and animals into the water are elements which communicate and regulate the activity of the community, modifying the numbers of individuals of the species. They may be attractants, repellents, may facilitate the development of certain species and suppress others, etc. These allelopathic relationships are well known in continental phytocenoses, vertebrates and insects as well. The species-specificity of metabolic signals in certain cases has been experimentally proven. Lukas (1964) referred to this type of relationship as nonpredatory ecologic connection. These connections are achieved by chemical agents with a broad spectrum of action which, after they are liberated into the water, become an environmental factor for the organisms in the community. Exocrines may be products of excretion or of decomposition of organisms.

Some marine bacteria excrete metabolites which are toxic for algae, thus changing the population of the latter (Berland et al., 1972). In water rich in diatoms, the population of blue-green algae will not be great (Marumo, Asaoka, 1974). The excreted metabolites can be considered for neighboring organisms a method of adaptation to the interrelationships in the community. This type of metabolic interaction relates the population of the diatom *Skeletonema costatum* and the flagellate *Olisthodiscus luteus* (Pratt, 1966). In a medium favorable for both species, they cannot achieve simultaneous abundance. The advantage will go to that species, the cells of which begin intensive division with larger numbers or at a younger phase of the population. The substance excreted by the flagellates simulates cell division of the *Skeletonema* in a rarefied culture of diatoms, and depresses cell division in a compact culture. In a community, these species have different survival strategies, which can be interpreted as behavior in the broadest sense: The diatom must "try" to begin its first division with a large number of cells; the flagellate conducts "chemical warfare" with it. The *Skeletonema* may suppress (or stimulate) the growth of bacterial cells as well (Bé et al., 1974).

Suppression of a competing species by means of "chemical weapons" is a common occurrence in the sea. When the hydroids *Hydractinia echinata* and *Podocoryne carnea* are simultaneously cultivated, their stolons never interweave, and after a certain period of time, *Podocoryne* completely suppresses the growth of *Hydractinia* (Gallien, Govaere, 1974). The same type of interaction, but intraspecific, may regulate the number of individuals in clusters of the hydromedusa *Tiaropsis multicirrata* (Zelickman, 1969; Zelickman et al., 1969).

Succession itself may be, to a significant extent, a result of dynamic integration (inhibition of neighbors or self-inhibition) of the community, mediated by exocrines. This aspect of the significance of free metabolites facilitates the development of new connections between species and the occupation of new habitats. The exocrines indirectly regulate the populations, marking out the path of migrants, facilitating encounters between the sexes, unmasking prey, marking spots for settling of larvae, etc. This indicator role of external metabolites is no less significant than the "plus-minus interaction" reactions mentioned above.

3.2 Pheromone Regulation

The steroid compounds, the derivatives of which usually serve as moulting and juvenile hormones, as well as sexual pheromones, are inherent in all types of invertebrates. Pheromone regulation, in particular, is one type of exocrine regulation. When in the process of evolution specialized receptors developed on the one hand and, on the other hand, the hormones of the donor began to be liberated into the environment, communication by means of pheromones became possible (Kittredge, Takahashi, 1972). The sexual pheromones have been most thoroughly studied to date. It is possible that they appeared earliest in the course of evolution. Usually, a sexual pheromone is a relatively species-nonspecific substance liberated into the water, causing swarming of individuals of both sexes and subsequent emission of reproductive products, e.g., in the polychete *Platynereis dumerilii* (Boilly-Marer, 1969). In the polychete *Ophryotrocha puerilis*, sexually mature females liberate into the water a substance which stimulates the development of male sexual characteristics in immature individuals. The females of many nereids excrete species-specific substances which accelerate the discarding of sperm by the males. The males of the polychete *Grubea clavata* produce a substance which facilitates emission of eggs; without this substance, the eggs are resorbed in the bodies of the females. The ability to attract males or females, preferably of only the same species, is evolutionarily more progressive; this occurs, for example, in the gastropod *Littorina littorea* (Dinter, 1974).

The species specificity of sexual pheromones is relative and does not assure complete reproductive isolation. For example, males of the copepod *Eurytemora affinis* demonstrate searching sexual behavior and "chase" not only females of their own species, but also females of *E. herdmani* and *Pseudodiaptomus coronatus*. However, the males of the latter two species demonstrate sexual behavior only toward females of their own species (Katona, 1973). The searching behavior of *Calanus* and *Pseudocalanus* is equally expedient (Griffiths, Frost, 1976).

Even in the decapods, the larval hormones and sexual pheromones have still not completely biochemically diverged. The crustecdyson of the decapods usually acts as a pheromone in combination with any other pheromone, causing onset of the stage of maturation of the female. The females of *Homarus americanus*, just after ecdysis, liberate a pheromone which suppresses the aggressiveness of the males and provokes sexual behavior in them. However, if females are forced to moult by removal of the eye stalks, the water from an aquarium containing these females causes only mild manifestation of searching sexual activity. When males contact females which have not moulted, only aggressive behavior is manifested (Atema, Engstrom, 1971). The males of many crabs, e.g., *Carcinus maenas*, *Macropipus holsatus* and others (Eales, 1974), assume the mating position only in the presence of females which have recently moulted or are in the premoulting stage. The pheromone is species-specific and is excreted with the urine.

Thus, the contact of the sexes at the biologically most favorable time, and reproductive isolation are assured in many cases by the chemical communication channel. The functions of this channel, the end result of which is aggregation of the animals, have many aspects, like all manifestations of topic connection. One means of aggregation is excretion by mature animals of substances which stimulate settling of meroplanktonic larvae. The larvae of barnacles, in which this phenomenon was demonstrated for the first time (Crisp, Meadows, 1963), respond only to the "settlement factor" if it is found on a surface suitable for settlement in all its parameters.

The benthic predators frequently excrete substances which "mark" the place where prey is found. Thus, hungry *Acanthaster planci* sea stars move more rapidly toward coral (their only food) on which *A. planci* are already feeding (Ormond et al., 1973).

Chemotactic communication as a means of recognizing individuals of one's own species (not necessarily of the opposite sex) results in the formation of aggregations and also acts as a mechanism for regulation of numbers. This is well known in the planaria. *Phagocata gracilis* and *Cura foremani*, mixed together in a single vessel to the point of random distribution, regroup in single-species clusters quite rapidly. The adaptive value of this form of behavior consists in that *P. gracilis* lays its egg capsules only in clusters of at least 200 individuals (Reynierse, 1967; Reynierse et al., 1969). *Dugesia tigrina* spontaneously decapitates when greatly crowded--one individual per 10 ml of culture fluid. It is assumed that the metabolite causing this phenomenon suppresses asexual reproduction of the planaria, replacing the neurohumoral stimulus for reproduction (Vowinckel et al., 1970).

Frequently, the level of activity of an animal and its diurnal rhythm depend on the number of individuals in the group, increasing with increasing number of individuals up to a certain limit, then sometimes decreasing. The manifestations of the group effect are various, although the mechanism of the phenomenon itself is frequently unclear. For example, in males of the gastropod mollusks *Crepidula fornicata*, joining of the mollusks into chains of several individuals activates the growth of all the individuals except for the uppermost male, the growth rate of which is the same as that of an isolated male (Le Gall, 1973). In a mixed culture of three species of Black Sea mollusks, the oxygen consumption and growth rate were both lower than for single-species cultivation under the same conditions (Kiseleva, 1974). In any case, the metabolites have a direct relationship to the regulation of growth of the members of a community.

Maintenance of nongregarious burrowing animals, *Homarus americanus*, in a group for some time subsequently decreased the aggressiveness of these individuals when they were placed individually into aquariums with one *Homarus* and one place of refuge (Dunham, 1972). "Swarming pheromones" similar to those of many insects have been found in crustaceans: They are present in *Saron marmoratus* and many hermit crabs (Hazlett, 1966). Thus, the group effect and mass effect are manifestations of the initial phases of formation of nontrophic group communication.

Chemical protective substances, temporarily blocking the mobility of an enemy, are known in plankters. For example, the medusa *Aequorea aequorea* excretes a substance which inhibits the movement of the medusa *Stomotoca atra* (Lenhoff, 1964), which frequently eat coelenterates. One variety of protective pheromone is the alarm substance, which is also quite widespread among aquatic invertebrates. If viscera of the sea urchin *Diadema antillarum* contact the water, a substance is liberated which causes other sea urchins to flee the area of danger.

One special type of intraspecies signaling, intended to aid in nocturnal visual reception, is bioluminescence. In females of the euphausiid *Meganyctiphanes norvegica*, the periods of maximum response to the luminescent flashes of the males correspond with the periods of attachment of the spermatophores; thus, luminescence can be looked upon in this case as an attribute of sexual behavior (preparedness signal). Imitative (response) luminescence has been detected in the same animals (Kay, 1965; Tett, 1972). In the ctenophorans *Beroe* and *Bolinopsis* and the hydromedusa *Aeginopsis laurentiae*, a flash can cause a defensive motor reaction (Labas, 1973).

3.3 Interspecific Collective (Group) Reactions

Group reactions which tend to support coexistence of species due to negative contacts can be considered aggressive relationships. These relationships are possible when the ability to recognize objects in the surrounding world is developed. The most primitive form of collective behavior is direct destruction of the neighboring species not for the purpose of eating it. Recognition of the object in this case apparently is chemoreceptor mediated. By this method, the madrepore corals, secondary in terms of abundance, which construct relatively small and slowly growing corallites, protect themselves from the dominant, more rapidly growing forms: the more aggressive, slowly growing species destroys the polyps of the other species, dissolving their tissues with mesenterial threads (Lang, 1973). This is a simple case of group behavior with a direct topic (to use the terminology of V. N. Beklemishev, 1951) connection. However, the coral reef biotope is also the site of indirect connections. A complex form of group interspecies behavior with indirect topic and phoric connections is seen in the relationship between fish and sea anemones and between hermit crabs and sea anemones. The symbiotic relationship between the fish *Pomacentridae* and the sea anemones of the family *Stoichactidae* is well known (Dhont, 1971; Mariscal, 1970). Frequently, one corallite, one sea anemone, the mantle cavity of one tridacna or one sponge osculum is occupied by a single pair of fish, shrimp or crabs, monopolizing the tiny microbiotope.

Sometimes one corallite is inhabited by a single pair of crabs of one species, which is achieved by intraspecies agonistic behavior (Preston, 1973). Twelve species of fish of the genus Amphiprion are obligate symbionts, exhibiting territorial behavior (protection of "their" sea anemone as long as they are located near it). If the anemone is removed, the territorial behavior decreases, and the feeding and aggressive forms of behavior are altered. The closeness of direct and indirect topic and phoric interdependence can be quite varied; for example, in the various species of Amphiprion or among shrimp from the families Hyppolytidae, Alpheidae and Palaemonidae, associated with a broad range of benthic invertebrates and even pelagic scyphomedusan (Bruce, 1972; Fankboner, 1972).

In representatives of the mobile epifauna, the primitive form of collective reactions is rather passive. Thus, the brittle stars Astroboa nuda form unusually close settlements in the shallow waters of coral reefs. The arms of the individuals intertwine, forming a dense net across the direction of the current. This "plankton net" assures effective, nonselective filtration of the bottom-dwelling copepod (Tsurnamal, Marder, 1966). It has been shown that each star occupies the same position each night, and retreats to the same shelter each day (Fricke, 1973). Similar behavior is exhibited by Ophiothrix gracilis.

Any systematic encounter of individuals, resulting in a change in the course of individual motor reactions or combinations of motor reactions, must be considered an evolutionarily more advanced form of group ("social") behavior. Strictly speaking, nongroup, purely individual, behavior, in the precise sense of this word, cannot be achieved in nature, since some minimal interaction between individuals always occurs, at least in some stage of ontogenesis. However, obligatory group behavior is the most fully integrated form of living activity, though its population adaptiveness is not always obvious. This category of nontrophic connections must include all aspects of intra- and interspecific domination-subordination relationships (Wynne-Edwards, 1962), since they also regulate the size of populations and increase qualitative variety of genotypes due to complete or partial elimination of a number of "unsuitable" individuals from the breeding pool. Thus, after establishment of a hierarchy in a group of Diogenes pugilator hermit crabs, the dominant male eats more food and moults more frequently than the subordinate males (Rossi, 1971). In the Dardanus arrosor hermit crabs, living in symbiosis with the Calliactis parasitica sea anemone, the anemone is always captured by the dominant crab, regardless of whether it already has a symbiont on its shell or not. The subordinate crab does not take an anemone in the presence of the dominant crab, even if the shell of the dominant crab is already occupied by anemones, so that a free anemone has fallen to the bottom (Mainardi, Rossi, 1969). In the squid Loligo pealei, a hierarchical structure of behavior of the males during breeding is observed. When there are more males than females, the subordinate males are not allowed to mate. The hierarchical behavior is not manifested during feeding (Arnold, 1962).

Competition between an individual and a group is frequently replaced by ritualized behavioral elements, a sort of "psychic attack" (Severtsov, 1951, p. 94). Ritualization is useful to the species, since it retains the most reproductively valuable males. There is another means for elimination of the contradiction: inter- and intra-species aggressiveness helps to scatter individuals over the maximum number of microbiotopes within the limits of their area of distribution. Ritualization is highly differentiated in decapods and, in a number of ways, is comparable to that of birds (Hazlett, 1972b). The hierarchy within a population arises in the process of aggressive collisions between animals, but after it is established, battles, as in the vertebrates, are replaced by ritualized behavior. The previous group contacts among decapods are important for the results of encounters between males: If in a previous battle a male won, it is probable that he will win again in a later battle with an opponent of equal size. Superior size, initiative in beginning the conflict and the experience of previous victories increase the chances of success in encounters (Mainardi, Rossi, 1972; Rubenstein, Hazlett, 1974). The position of the legs and claws during agonistic reactions in the crabs *Microphrys bicornutus* are more strictly fixed than during walking and feeding, allowing the crab to recognize the intentions of the enemy, by comparing its behavior with the stereotype (Hazlett, 1972a). The strategy of the victor in a battle between hermit crabs consists in the best possible adaptation of his own behavior to the behavior of the enemy, while the behavior of the loser always contains greater elements of chance (Hazlett, Estabrook, 1974).

However, true battles arise (for example, among *Callinectes sapidus*) only when ritualized attempts to stop a crab approaching food or a female are unsuccessful (Jachowski, 1974). Ritualized aggressive behavior for the protection of individual territory is clearly expressed even in certain individual species with no hierarchy, such as *Munida sarsi* (Berrill, 1970). The degree of correlation between ritualized behavior and the defense of the territory, may change as a function of local conditions. For example, *Dardanus arrosor*, after losing its sea anemone, is more frequently attacked by other members of the same species. When there is a shortage of food or an increase in the number of crabs, they more frequently place an anemone on their shell. After many months in an aquarium, hermit crabs lost their anemone-seeking activity, but when an octopus was placed in the aquarium, this behavior was reactivated (Balasch, Mengual, 1974). Aggressiveness is differentiated with respect to mature and young animals, a behavioral adaptation to protection from cannibalism. For example, in the hermit crab *Clibanarius vittatus*, if there are great differences in the sizes of two individuals, the larger crab often simply ignores the smaller one (Hazlett, 1968).

Relationships in a group are not always aggressive in nature. The decrease in aggressiveness observed following long-term cohabitation of *Pagurus bernhardus*, with an outbreak of aggressive behavior toward a new individual, are apparently explained by the capacity for individual recognition (Hazlett, 1969). The shrimps *Hymenocera picta* live in pairs, generally of different sexes. A male and female usually sit side by side, side, undertaking no sexual activity and not feeding. The partners have a quieting effect on each other. Isolated males seek out only their own partner (Seibt, Wickler, 1972). The shrimp *Stenopus hispidus* fight to the death when they meet an individual of the same sex, but when a male and female meet, the female assumes the subordinate position, and a long-lasting pair is formed (V. R. Johnson, 1969). In this behavior we can see the primordial form of monogamy inherent in vertebrates, indicating the convergent evolution of behavioral mechanisms in various branches of the animal kingdom (Wickler, Seibt, 1972). Analysis of behavior as one aspect of ecologic adaptation (Reese, 1964; Fricke, 1973) shows that convergent evolution is unavoidable. Thus, aggressive behavior in species which are territorial should be suppressed for successful mating, which is achieved by the use of the subordinate pose by one of the partners, though the specific manifestations of this ritual in various taxonomic groups are different. General systems of behavior, characteristic for certain life forms, change, adapting to the specific demands of each species. Therefore, in highly specialized commensals, programming of behavior varies most widely from the general system. The specific manifestations of the general features of behavior depend greatly on the development of receptors. For example, in lower crustaceans and gastropods, ritualization (if it is present) depends to a greater extent on the perception of the chemical and vibrotactile stimuli than visual stimuli. Naturally, behavioral adaptations are particularly complex in very complex biotopes with sympatric speciation.

The trigger mechanisms of group reactions may depend on any receptor system. The key stimulus may be either an abiotic signal or information from another organism. The capability for group reactions may be initiated by the diurnal rhythm of abiotic factors. For example, the distribution of male *Uca pugilator* crabs is group-determined before the tide flows, while during the flow of the tide it is random; during tidal flow, the females form groups (Rajendran, 1974). Individual burrowing decapods *Goneplax rhomboides* and *Nephrops norvegicus* are usually active during the dark hours, but the presence of other individuals of the same species inhibits this activity (Atkinson, 1974). The presence of other individuals is also significant in other respects; disruption of territoriality, e.g., in lobsters, results in atypical migration, making them prey to predators (Chittleborough, 1974).

Orientation among other similar animals is a result of complex functioning of receptors; territorial behavior, as a variety of group behavior, does not always include continuous communication with another individual of the same species. Arbitrary interruptions in communication are permissible with wave translation. The reception of information by means of vibrotactile receptors is widespread. It is in this manner that sagittae detect Copepoda: The hunting sagitta hangs motionless in the water until it senses vibrations at a specific frequency. Possibly, each species of chaetognaths has its own specific range of perceived frequencies (Newbury, 1972). In the land crab *Gecarcinus lateralis*, intraspecies communication is achieved by the vibration of the substrate by each individual with a definite sequence of pulses (Klaassen, 1973). The *Ocypode* crabs also react to vibrations of the substrate, emitting response signals at the corresponding frequency (Horch, Salmon, 1972). The threshold frequency for beating of the barnacles is species-specific; therefore, representatives of different species respond differently to the identical stimulus, allowing them to coexist (Blaker et al., 1964). It has been experimentally shown that in Balanus improvisus, information on the condition of a neighbor influences the mechanoreceptors, the micropopulation "tuning" itself to the rhythm of beating of the most active individual (Vilenkin, Vilenkina, 1971; Vilenkin, Zaikin, 1975).

3.4 Intraspecific Structures of Behavior of a Group of Individuals

One means of avoiding competition where ecologic niches overlap is heterogeneity of the spatial distribution of micropopulations, hemipopulations or groups of other ranks with different types of behavior. Heterogeneity, in particular, may result from a group response to gradients in biotic or abiotic environmental conditions. These responses are most typical for nonpredatory animals. The most important methods of formation of discreteness probably differ in organisms of different sizes, but they all lead to an increase in the isolation of groups.

Schooling may disappear or appear under certain conditions. For example, the cladoceran Polyphemus pediculus, in an aquarium with sufficient food, normally live and breed individually, but in plankton live only in groups with very constant locations (Butorina, 1972). Butorina considers the group to be a food-hunting association of voracious predators feeding on prey which also live in groups. The group of predators includes individuals with identical spectra of prey, similar nutritional demands and compatible speed of movement. When the population density is low, these groups do not form (Luferov, 1970; Luferov, Stetsenko, 1971). Moina swim in fish-free areas in dense schools, simultaneously changing direction and retaining their order. However, in the presence of predatory fish, schools do not develop (D. S. Johnson, Chua, 1973).

Underwater observations have established the existence of schooling in the Copepoda Arcatia spinata, Oithona nana, O. oculata, Farranula gracilis and others (Emery, 1968). A school of Farranula gracilis acts like a single individual and holds its position against the current. If alarmed, the animals scatter, but then the school reforms. The density of Copepoda in the school may be as high as 10^5 indiv./m^3.

The reasons and mechanisms of formations of clusters, aggregations and schools differ for different forms of life, and also for large and small organisms. For nonselective filter-feeders--Appendicularia--which seem to be poor swimmers, the "collective force" may create local hydrodynamic factors, simultaneously facilitating increases in phytoplankton concentration. Clusters of Oikopleura dioica (concentration on the order of 10^4 indiv./m^3) have been described several meters wide and several kilometers long, developing in the region of a phytoplankton bloom (Seki, 1973). Clusters of Oikopleura frequently form parallel strips up to 30 m long, with a width and depth of a few centimeters. Owen (1967) considers small-scale horizontal surface vortices which develop at lines of convergence, i.e., Langmuir circulation, to be responsible for these clusters. It is possible that the movement of these strips of Oikopleura helps to reduce the resistance of the water, due to the mucus which the animals excrete.

The overwhelming majority of species of Copepoda and Ostracoda show a tendency to aggregation (Fasham et al., 1974). Aggregations* may be differentiated depending on sex, age and physiologic condition of individuals. In the copepod Epilabidocera amphitrites, accumulations of the crustaceans near the surface of the water consist only of males, which differ from the females in that they exhibit phototaxis (Park, 1966). In Metridia longa, the microdistribution of the older copepodites differs from the distribution of sexually mature individuals, which inhabit the same layer of water (Romanovskiy, Chusova, 1974). Doubtless, this sort of heterogeneity is adaptive. An example is the Monstrilloida, semiparasites of sublittoral invertebrates. Their hosts live in clusters, and it is not surprising that the crustaceans themselves are also clusterers. The grouping of hosts helps the nauplii to find hosts, while the grouping of the monstrilloidae themselves facilitates simultaneous emission of nauplii and their settlement (Isaac, 1974). This increases the level of inbreeding in the population, which in turn facilitates sympatric speciation, i.e., the development of heterogeneity at a higher level.

Among the Decapoda, schooling is widespread, the characteristics of the school being frequently quite homogeneous. Schooling is most common among surface-dwelling species, for example, the shrimp Sergestes similis, which forms accumulations with densities of up to 4500 indiv./m^3 (Omori et al., 1972).

Mixed aggregations are also found, consisting of individuals of various species, e.g., the shrimp Acetes kochinensis and various genera of amphipods (Achuthankutty et al., 1973). The reasons for formation of this type of aggregation are not clear. In the pelagic crabs Polybius henslowi and Charybdis edwardsi, surface schools contain individuals of both sexes, oriented against the current and precisely observing their distance (J. A. Allen, 1968; Della Croce, 1961; Della Croce, Holthuis, 1964, 1965; Rice, 1969). Another method of observation of distance is the movement of crustaceans in chains during seasonal migrations of the Stomatopoda Oratosquilla investigatoris (Losse, Merrett, 1971) and the lobster Panulirus argus (Herrnkind et al., 1973). The lobsters move one after another, with their antennae or pereopods touching the abdomen or tail of the lobster in front; a single column may include as many as 65 individuals. During brief stops, the lobsters also stay in an organized cluster, e.g., a "rosette."

3.5 Adaptive Value of Schooling Reactions

The collective reactions of plankters, during which the school reorganizes or is restored, consist of a combination of behavioral events which take consideration of the behavior of neighbors.

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*The word "schooling," in our terminology is used to stress the active role of inner factors in forming an aggregation and the intensity of interdependence between the individuals.

Schooling is related to the manifestation of stereotypic reactions based on signal simplicity, speed and accuracy of action. Manifestations of schooling behavior in pelagic animals of various taxons have a great deal in common. The information which supports the schooling behavior can pass through many channels. The motivation may also be varied. Defensive motivation is most common: Schooling, an essentially little structured system of behavior, is a useful defensive response when pelagic animals are under attack by predators. The sequence of motor events is adaptive and constant for the group, but the trigger (liberating) stimulus for these behavioral programs can vary. It is assumed that the formation of groups of any repetitive type is a manifestation of protective reactions. Attempts to analyze schooling experimentally (Radakov, 1972; Neill, Cullen, 1974 and others) have shown that schools definitely play a protective role among prey animals. Among predacious fish, squids (*Loligo vulgaris*) and cuttlefish (*Sepia officinalis*), the absolute and relative number of successful attacks on the prey decrease as the number of fish in the field of vision of the predator increases. An increase in the number of fish (prey) in a school retards the beginning of the attack and makes the capture of prey by attackers more difficult. Schooling of the prey dissipates the attention of the predator, confusing the stereotype sequence of the individual stages of the chase, and the attack is frequently not completed. The usefulness of the school when the predators are herding types has been proven for squid (review: Nesis, 1975) and fish (Radakov, 1972).

Let us discuss the phenomenon of schooling in euphausiids and mysids, in which it is frequently seen and has been relatively well studied, in somewhat more detail.

Among the euphausiids, phytophages predominate: *Thysanoessa longipes*, *T. inermis*, *T. raschii*, *Meganyctiphanes norvegica*, *Euphausia superba*, *E. crystallorophias*, *E. vallentini* (Zelickman, 1961b, 1968b; Marr, 1962), forming schools and clusters near the surface. A euphausiid school is a practically single-species organized group of animals, recognizing each other (maintaining distance), of relatively homogeneous physiologic structure. Among Barents Sea euphausiids, as exceptions, we observed three-species schools, but always one species dominated. In most cases, the term "school" is applied only to mature individuals. A school may be scattered by external actions, after which it immediately reforms. The dimensions of a school vary from a few meters (Nemoto et al., 1969) to 30-100 m and greater (Pavlov, 1974; Marr, 1962; Nemoto et al., 1969). The shape of schools of *Euphausia pacifica*, *E. similis*, *E. nana*, *T. inermis*, according to Nemoto, is species-specific. It seems to us that the larger the crustaceans, the larger the size of the school. The largest schools, doubtless, are those of *E. superba*; the concentration in the school is up to 100 kg/m^3 (Marr, 1962; Nemoto, 1968). School formation in euphausiids is an active process (Zelickman, 1960a, 1961b; Zelickman, 1961), probably resulting from a combination of causes. We consider school formation in euphausiids to be a characteristic primarily of phytophages, which cast their spawn into the water; the young of these species begin to feed on phytoplankton in the first calyptopis stage. School formation occurs in the regions where the young will feed; in any case, during the spring and summer biologic season in the Arctic and, apparently, Antarctic waters, schools are always observed in areas with abundant plankton. It is not clear whether true schooling occurs in euphausiids with predatory and mixed feeding habits. Large aggregations are occasionally formed by Thysanoessa longicaudata (Forsyth, Jones, 1966), Euphausia diomedae and Stylocheiron abbreviatum (Roger, 1974), but these data, based on extended catches, do not prove that what was encountered was a true school, rather than a simple accumulation with an unknown degree of integration.

Schooling is seen in most massive species of mysids (Mauchline, 1971). Schools of Leptomysis linguura may be quite permanent and remain almost every day in the same place. Schooling is observed in L. mediterranea and Siriella armata only in the day, particularly if there is a gradient of illumination. Schools of L. linguura simultaneously contain individuals with different photoactivation (Macquart-Moulin, 1971, 1973; Macquart-Moulin, Patriti, 1966). Schools of Mysidium gracile find shelter among the spines of the sea urchin diadema antillarum (Emery, 1968). Fish never capture mysids from these schools.

The characteristics of schooling and the behavior of mysids in a school agree in basic features among the various species (Zelickman, 1974; Zelickman, 1975); the behavior of mysids and euphausiids is similar to the behavior of fish in a school as described by Radakov (1972). The orientation of individuals in a school and observation of spacing are apparently maintained by the optomotor and kinesthetic systems of orientation. The forms of integration of groups of mysids and other crustaceans which have been observed permit their behavior to be interpreted as an integral, complex reaction of the organisms, rather than simply an ensemble of kineses and taxes. The mechanism of orientation of the mysids is probably governed by the level of illumination, the position of the light source, its polarity and, possibly, spectral characteristics; no less important is distance perception--the location of fluctuating movements of the water, at least for species which school in darkness. It is possible that various reception systems function simultaneously, with an overall coordinator. There is every reason to assume, for example, synergy of receptor perceptions in hermit crabs (Hazlett, 1970).

We must not consider the heterogeneity of physical characteristics of the aquatic medium the primary cause of the high degree of organization of groups of animals, particularly crustaceans, both in nature and under experimental conditions. The adaptive capabilities of schooling behavior among crustaceans can be compared to selective advantages which arise upon schooling of fish. These advantages must entail evolutionary optimization of the collective reactions of animals favorable to the population. These collective reactions are most useful to massive species subject to predation, and are also necessary in situations requiring movement of entire populations, e.g., spawning migrations. What are the parameters which must be optimized in order to preserve a population? In this case, one of the semiquantitative abstract models (Vine, 1971) of differentiation of the hunting behavior of a "visual predator" as a function of the type of distribution of prey seems applicable. This model considers a situation in which the prey, of identical size, is attacked by a predator, which is located either within or outside the population of prey and scans the visible space in order to locate its prey. The strategy of the prey should be optimized with respect to a number of criteria--maximum individual and group safety, minimum probability of pursuit, maximization of the time required for detection and capture. Vine showed that in this situation, it is most favorable to the prey to be evenly distributed in a circle; within a circle, the prey should form an arc so that the head of the rearmost individual is directed toward the tail of the foremost individual. The greatest individual safety will be achieved by individuals in an ordered pattern around the periphery of a sector or at the center of a chain. Schools which can observe in all directions see predators most easily and can restructure themselves most quickly. The "nose to tail" position is favorable for the group of prey as a whole. Some of the advantages of schooling are also gained by each individual, e.g., when the predator hunts by individual capture of prey, it is favorable to increase the size of the school (minimize the size of the target prey). The adaptive results of schooling following from the geometry of the constructions of Vine, agree with field observations (J. A. Allen, 1968; Della Crose, Holthius, 1965; Herrnkind et al., 1973; Losse, Merrett, 1971; Emery, 1968) and experiments (Steven, 1961; Clutter, 1969; Zelickman, 1974, etc.). Of course, other principles of configuration and geometry of the school are possible, e.g., when interacting with a prey, orientation by chemoreceptors, during sexual interactions, behavioral interactions, etc. However, a given geometry of spatial organization of individuals of the same species as a method of decreasing predation is doubtless one of the most probable adaptive structures of this behavior.

In those cases when many prey individuals are absorbed at the same time, e.g., when whales feed on swarms of Euphausia superba, the train of argument presented above might seem inapplicable. However, one should recall that swarms of E. superba vary greatly in size. The mosaic-like distribution of the prey and the rapidity of restructuring of swarms fatigue the predator and, probably, make the search for the prey much more difficult.

Thus, the types of nontrophic connection in a community have as many aspects as the competition for food, and are based on the purposes which are common for all bonds in populations: spatial and reproductive isolation, elimination of nonviable genomes from the breeding stock, weakening (by ritualization, pheromone regulation, etc.) of intraspecies and interspecies interactions which are too active. Essentially, the etiologic bonds are equivalent to communication lines among individuals of the same or different ages, one or both sexes, between generations and populations. Intraspecific and interspecific communications have evolved from a single-bit information system to a multiple-bit system (Sebeok, 1969). In the sea, this path is the same as on land. From external metabolites as the simplest carriers of information, species go over to the utilization of other channels for information transmission--the vibrotactile, visual and acoustical channels. The information capacity of the etiologic signaling also increases; in hermit crabs, lobsters and crabs it may be as great as in social insects and birds (Hazlett, Bossert, 1965; Hazlett, 1972b; Hazlett, Estabrook, 1974). The development of the ability to recognize patterns leads, on the one hand, to greater individualization and complication of etograms and, on the other hand, to the development of schooling behavior as a system of adaptation of the population as a whole. The complication of the etiologic integrative elements observed in any community of free-living organisms, like the strengthening of their significance in a phylogenetic sequence, is a process which occurs in parallel to the creation of the second signal system in man.

CHAPTER II. PELAGIC COMMUNITIES AND THEIR STRUCTURAL AND FUNCTIONAL CHARACTERISTICS

1. Trophic Relationships in the Pelagic Zone

(M. E. Vinogradov, N. V. Parin, A. G. Timonin)

Primary sources of matter and energy. The trophic relationships in the pelagic zone of the ocean, in spite of their great importance for an understanding of the functioning of communities, have been quite insufficiently studied. Even such a basic problem as the primary sources of incoming organic matter (energy) entering the food chain of the communities which, in the final analysis, determines their total productivity, functioning and structure, is still a subject of lively debate.

The primary organic matter in the pelagic zone is formed by the photosynthetic activity of phytoplankton. It is thought that the entire food pyramid is constructed on this basis. The flow of energy passes through the phytoplankton to the herbivorous zooplankton, then to the carnivorous plankton and nekton (Fig. 1a). However, attempts at quantitative estimation of the energy flow and energy balance of the various trophic levels have shown that over broad expanses of water in the oligotrophic regions of the tropical ocean, this path cannot support the energy demands for existence of the communities. At least in these regions, obviously, another path of arrival of energy is no less important--through autochthonous and allochthonous dissolved organic matter to bacteria, protozoa, then filtering and predaceous invertebrates (Fig. 1b). It is assumed here (Sorokin, 1971a) that the dissolved organic matter is formed in excess in the highly productive cold regions of the ocean, descends together with the descending flows of water into the deep layers where, due to the low temperature, its decomposition is retarded, then returns to the surface in the equatorial regions in the areas of quasi-stationary upwelling of water where, at the high temperatures reached in the surface layers, it becomes available for bacterial destruction. Thus, the bacteria in these tropic communities act as local "producers." Yu. I. Sorokin (1971a) believes that the bacterial path of inclusion of organic matter in the food chain in tropical communities is equal, in terms of energy flux, to the classical phytoplankton path, or even exceeds it. This high evaluation is not agreed with by all (Steemann Nielsen, 1972; Banse, 1974), but, nevertheless, the significance of the role of arrival of energy in the community through dissolved organic matter and bacterioplankton is obvious.

The trophic network of the community. The distribution of matter and energy among trophic groups in the community follows a complex network of trophic connections. Connections at the higher trophic levels may be comparatively easily traced by examining the contents of the guts of

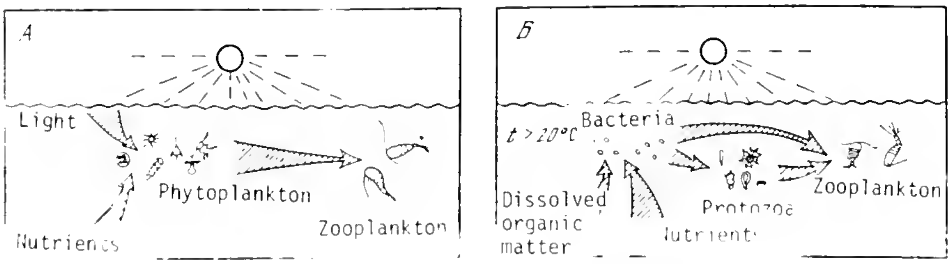


Fig. 1 Paths of arrival of organic matter (energy) into the food chain of communities. A, "pasture" food chain; B. "detrital" food chain.

predators. It is more difficult to evaluate the food chains of the smaller animals at the lower levels--those which suck out only the contents of the bodies of their prey, or which feed on small organisms without skeletons (e.g., protozoa) or bacteria. Analysis of the food's remains in their food lump is not sufficient to indicate the spectrum of their nutrition. In this case, other methods must be used for the investigation--study of the morphologic-functional peculiarities of the feeding apparatus, experimental feeding using various food labeled with C^{14}, direct observation under experimental conditions of the nature and intensity of feeding.

Within the food network, we can distinguish a number of trophic levels: primary producers of organic matter (phytoplankton); phytophagous pelagic animals: many copepos and euphausiid crustaceans, mollusks, some (few) fish; predators which feed on phytophagous animals--first-order predators (many copepods crustaceans, chaetognaths, amphipods, etc.); larger, second-order predators (decapods, small planktophagous fish, baleen whales); third-order predators--basically small fish and cephalopods, marine birds and reptiles; fourth-order and higher-order predators--medium-sized and large bony fish (tuna, alepisauri, etc.), sharks and the toothed whales. The total number of trophic levels may reach seven in extreme cases, the four upper levels consisting entirely of nekton (Parin, 1968, 1970). Upon transition from each lower level to the next higher level, an average of about 90% of the energy is lost.

Since the food connections in a community are quite complex and variable, the distinction of trophic levels is quite arbitrary. Actually, the diet of many predaceous forms at the lower levels may include phytoplankton; second and third-order predators eat both predaceous and phytophagous animals; some squids and predaceous fish, occupying the upper levels of the trophic network (particularly the bugeye and yellowfin tuna) act as euryphages, eating anything of the appropriate size--from euphausiids to squid and fish. Depending on the presence or abundance of any of these items, their significance as a part of the diet may change significantly.

In spite of the instability of the separation of individual trophic levels in a community, their number, i.e., the length of the food chain, may differ significantly from community to community. This is determined, in the final analysis, by the varying stability of the communities which, according to MacArthur (1955), increases as the number of links in the food chain increases. High stability of a community, according to Margalef (1968), allows it to exist with a lower specific quantity of energy entering the system, i.e., with more limited food resources.

In the oligotrophic tropical or deep-water communities, the number of trophic levels is high, while in regions with a high level of primary production, the food chains of the communities are very short. For example, in the ultraeutrophic waters of the Peruvian coastal upwelling, the trophic chain of the pelagic zone community consists of only two main links: the phytoplankton and the anchovies. The presence of mass species of fish feeding directly on the phytoplankton is also characteristic for other subtropical, highly productive upwellings. During certain periods, phytoplankton dominates in the food of *Sardinella aurita* in the upwelling off northwest Africa, for *Sardinops melanosticta* and *Engraulis japonicus* off the Pacific coast of Japan, and for *Sardinops caerulea* in the Oregon upwelling, etc.

The trophic structure of communities in various climatic zones. The basic differences between subpolar and tropical regions of the ocean is that in the former there are great seasonal changes in the environmental conditions--the intensity of solar radiation, temperature, stratification of surface waters--whereas in the tropics, these factors change little. These planetary distinctions, in the final analysis, also determine the difference in the trophic structure of communities.

The trophic systems of communities in cold water and temperate to cold water regions are adapted to achieve the most effective utilization of the comparatively brief but clearly expressed spring maximum in biomass of phytoplankton, whereas in open regions in the tropical ocean, the system is adapted to achieve most complete utilization of the relatively low, but little changing level of production of phytoplankton throughout the year.

In Arctic, boreal and Antarctic regions, the main producers are the diatoms. Their primary consumers are copepods, euphausiids and (in certain regions) pteropod mollusks. Zooplankton is consumed by coelenterates, carnivorous copepods, hyperiids, chaetognaths, baleen whales and planktophagous fish. These fish, in turn, are eaten by predatory fish and squids (Fig. 2, A).

In the open regions of the ocean at low latitudes, the picture of trophic interactions in a community is much more complex (Fig. 2. B). The primary sources of food are phytoplankton and bacteria. In addition to the small phytophagous plankton, macroplanktonic predators are very important, serving as the primary food of planktophagous fish which, in turn, are eaten by larger predaceous fish, while these, in turn, are eaten by tuna and sharks (Parin, 1968, King, Ikehara, 1956, etc.).

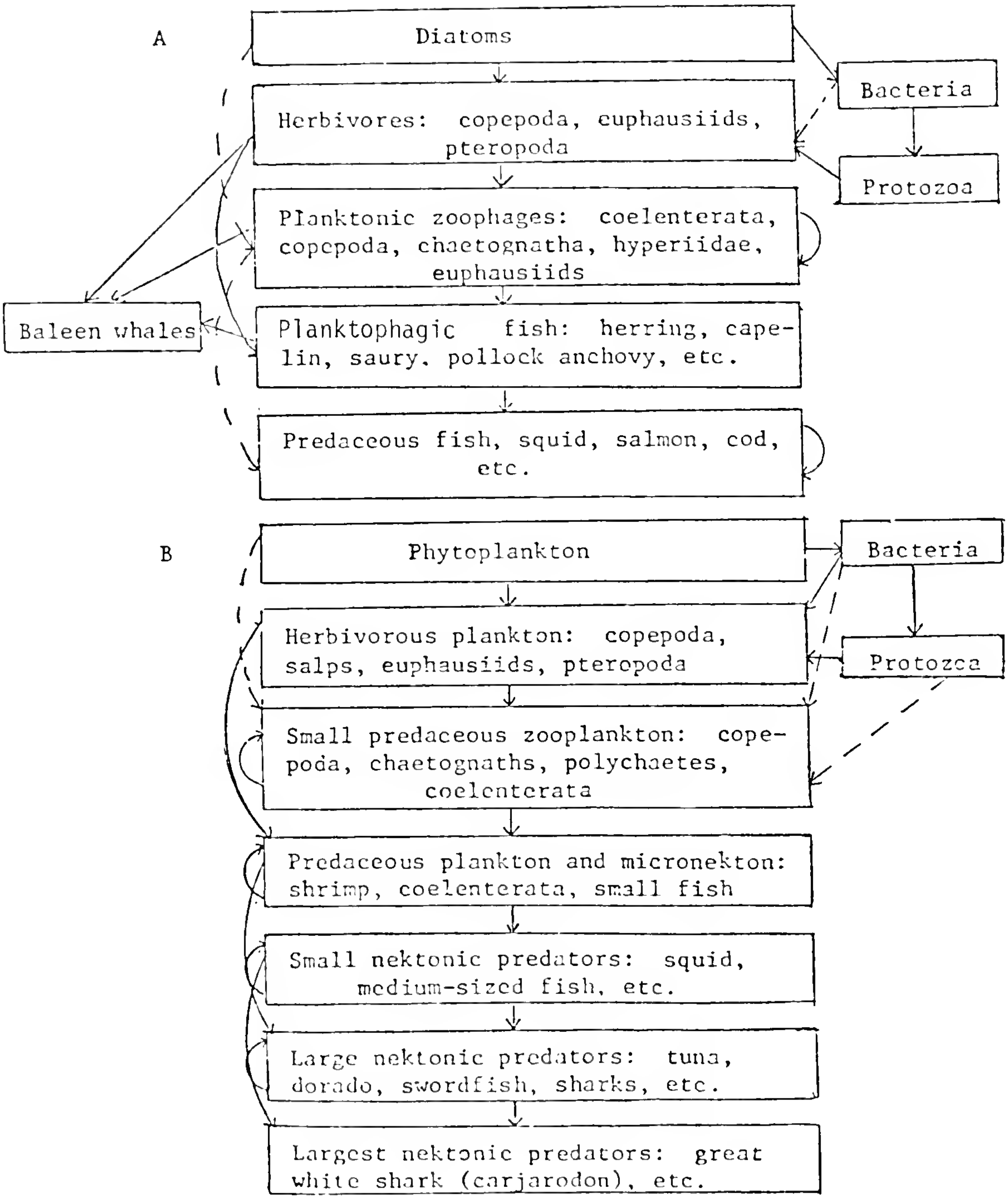


Fig. 2. Flow charts of basic food chains in polar and temperate (A) and tropical (B) areas of the ocean.

However, in the more productive regions of the lower latitudes in quasi-stable upwelling zones, the trophic structure of the community is significantly different: The food chain consists of a few links, sometimes even a smaller number than in the productive regions in the higher latitudes. These communities, with their short food chains and rigidly determined direction of the flow of matter and energy, yield extremely high production of the final links (fish), but their stability is quite low. The communities cannot react flexibly to significant changes in production of one of the links in the chain and, for example, a sudden decrease in production of the first link (phytoplankton) leads to truly catastrophic results. Examples include the well-known periodic disruption of the structure of the ecosystem of the Peruvian upwelling during "El Niño," causing catastrophic decreases in the catches of anchovy, deaths of hundreds of thousands of fish-eating birds, etc.

The communities of productive regions in the higher latitudes have special adaptations to the annual (and, of course, seasonal) fluctuations in the production of phytoplankton and therefore, even with significant changes in the population of the primary producers or consumers from year to year, catastrophic disruptions of their structure do not occur.

Changes in food interactions during development of communities. Marine pelagic communities, like sea-floor communities or continental communities, undergo significant structural changes from the moment of their formation until they reach the mature stage. The initial stages in the formation of communities occur with mineral forms of nutrients present in the photic layer. In this stage, the processes of accumulation of energy in the community prevail over processes of its dissipation.

As an ecosystem develops, the total content of nutrients in the water decreases to the extent that it causes a decrease in the biomass of phytoplankton and a change in its dimensional and systematic composition. Due to the different rates of maturation and achievement of maximum numbers of different trophic groups in the community, the entire trophic structure changes.

As the community matures, it is gradually carried downstream. Therefore, the time difference in achievement of the maximum development by the different trophic elements of the community leads to a shift in space, as well. Many observations in tropical regions in the Pacific and Indian Oceans have shown that the zones of maximum population of phytophages are usually long, narrow belts, crossing the oceans along lines of divergence. This, for example, is the distribution of _Undinula darwini_, the maximum of which in the Indian Ocean is found at the divergence at the boundary of the southern equatorial current and the equatorial countercurrent, and in the Pacific Ocean at the equatorial divergence (Vinogradov, Voronina, 1962, 1964).

The maximum population of mature carnivorous surface-dwelling copepods (_Euchaeta_, etc.), in contrast to the phytophages, is located parallel to the divergence, but displaced from it by 60-90 miles. Furthermore, in the Pacific Ocean, the maximum population of mature _U. darwini_ and

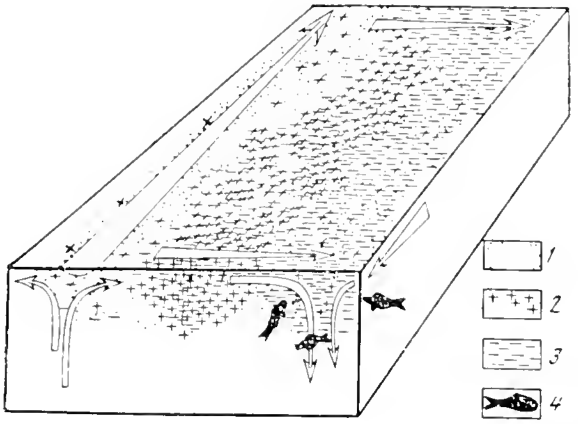


Fig. 3. Diagram of distribution of various trophic links of plankton and nekton in the zone of divergence and convergence near the equator. 1, phytoplankton; 2, phytophagous zooplankton; 3, predaceous zooplankton; 4, large fish.

Rhincalanus cornutus in the rich equatorial divergence is observed in two narrow strips along 0°30"-1°N and S latitude. Thus, as they grow, the crustaceans, which develop in the "juvenile" water, as it diverges, are carried north and south by the meridional components of the currents. The maximum of sexually mature individuals, however, is not shifted as far from the center as is the maximum of predaceous copepoda.

Naturally, the shift is greater, the longer the time of maturation of a species, the greater the speed of the current or the higher the position of the organism in the food chain. Therefore, accumulations of macroplankton and the large fish which feed on it, as a rule, are located to the side of a zone of divergence and usually fall along the nearest convergence, beyond which they cannot be carried by the meridional component of the equatorial currents (Fig. 3). In the equatorial zone, it is at these convergences that we observe the greatest accumulation of flying fish (Parin, 1968).

A. G. Timonin (1971) used the example of the tropical regions of the Indian Ocean to study the changes of the roles of various trophic groups, trophic and specific diversity in communities in regions with varying intensity of upwelling, i.e., varying degree of maturity of the population of the community (see Figs. 1, 2). The young communities in regions of intensive upwelling are characterized by high plankton biomass, low trophic and specific diversity, resulting from an increase in the total quantity of zooplankton due to domination by a few species. Filter feeders predominate (up to 58%), among these--coarse filter feeders such as Eucalanus attenuatus, E. subtenuis and Rhincalanus cornutus, which make up as much as 45% of the total biomass and 85% of the biomass of filter feeders. Predators represent 20-25% of the total mass of zooplankton. Where the water ascends upward more slowly, the total biomass of zooplankton is lower. Specific diversity increases, since the degree of domination by individual species decreases. The trophic structure becomes more diverse, but filter feeders still predominate, representing about 40% of the total biomass. The fraction of predators increases to 30-35%. Mature communities, in regions where upwelling is absent or where the water is descending, have low plankton biomass, high specific diversity, and weakly expressed domination of species. The trophic structure reaches almost its maximum possible diversity. Filter feeders amount to about 20-30% of the total biomass, and more than half of them are fine-filter feeders. The total quantity of predators increases to 45%. Analogously, in mesopelagic macroplankton in the mature communities of the central and western equatorial Pacific, the biomass is less, the specific variety significantly greater, than in the more juvenile communities of the eastern Pacific (Parin, 1976).

Factors which greatly shade the typical picture of distribution of trophic groups come into play in the higher levels of a trophic system. This results to a great extent from the fact that in the macroplankton and nekton of the open ocean, a large portion of the flow of energy is directed downward and beginning as low as the second or third level of consumers, a significant fraction of the total biomass is accounted for not by surface-dwelling, but by deeper dwelling, primarily mesopelagic, animals. The transformation of this flow on its path down into the depths has not been sufficiently studied, but subsurface currents apparently are quite significant in the redistribution of animals. Therefore, the spatial distribution of oceanic tuna, which make up the basis of an important industry, and of the toothed whales (particularly the sperm whales), feeding on mesopelagic fish and squid, cannot always be given an effective causal explanation from the point of view we are now considering.

Change in trophic structure of communities with depth. The change in the role of various trophic groups of mesoplankton with increasing depth will be analyzed on the example of the region of the Pacific Ocean near the Kuril Islands, since we have representative quantitative data on the vertical distribution of the entire mass of plankton and its basic taxonomic groups for this area (Table 1, Fig. 4).

The planktonic community, rich in phytoplankton, in the upper portion of the euphotic zone, is dominated by phytophagous filter feeders. In the lower levels of the euphotic zone, in the cold intermediate layer (100-200 m), the significance of predaceous species (primarily Sagitta elegans), feeding on animals from the surface layer, increases rapidly. The significance of filter feeders decreases, although it remains rather high as far down as 500-750 m. In the 500-1000 m layer, the significance of the euryphages increases, due to the development of a rather large number of radiolaria from the families Aulacanthidae and Aulosphaeridae at these depths, serving as a significant component of the diet of the euryphages, and also acting as predators of the copepods. Below 500-1000 m, the significance of the filter feeders decreases rapidly. The quantity of specific deep-water filter feeders is very small. The interzonal filter feeders, present in comparatively large numbers (primarily the copepods Calanus cristatus and C. plumchrus), feed in the producing zone and, apparently, do not feed in the deeper waters. Ignoring the interzonal phytophages, in the 1500-3000 m layer, the plankton consists 60-80% of zoophagous forms, primarily catching zoophages. Deeper than 3000-4000 m, given the very low plankton biomass and its great dispersion, predation, even passive predation, is apparently not energetically expedient, and the significance of zoophagous forms is greatly decreased. Euryphages move into first

Table 1. Change in significance of basic trophic groups of mesoplankton in Kuril region of the Pacific Ocean with depth in the summer of 1966 (% of total mass of mesoplankton in each level, ignoring interzonal filter feeders which do not feed at the depth where caught--after Vinogradov, 1968).

Depth, m	Filter feeders (phytophages and detritophages)	Catchers (zoophages--predators and scavengers)*	Euryphages
0-50	83	11	4
50-100	57	33	8
100-200	40	51	5
200-300	53	27	17
300-500	50	25	16
500-750	9	46	31
750-1000	11	47	29
1000-1500	4	66	16
1500-2000	2	74	13
2000-2500	3	86	8
2500-3000	5	6	22
3000-4000	3	32	46
4000-5000	3	15	50
5000-6000	1	9	51
6000-7000	1	1	37
>7000	4	14	31

*The biomass of predators is low, since we do not include the weight of coelenterates or of large cephalopods and fish which are not easily caught in plankton nets.

place, being able to utilize the greatest variety of food--living organisms, their remains and fecal matter, raining down from the overlying layers.

At 4000-6000 m depth, the significance of phytophages increases again, due to the presence of mysids of the genus Boreomysis. These mysids feed on phytoplankton in the surface layers, then descend to the deeper layers, where there are practically no predators, and the probability of their being eaten is greatly reduced. Studies performed on board the VITYAZ have shown that groups of Boreomysis incisa with stomachs packed with fragments of diatoms and Tintinoidea, are constantly observed at a depth of 4000-6000 m, sometimes slightly higher or lower (Vinogradov, 1970a). This indicates that there is regular, rapid transport of phytoplankton through a tremendous mass of water and emphasizes once more the importance of vertical migration in the transportation of organic matter from the productive zone to the depths of the ocean. Almost the entire mass of copepods at these depths consists of euryphages. Deeper than 6000 m, the

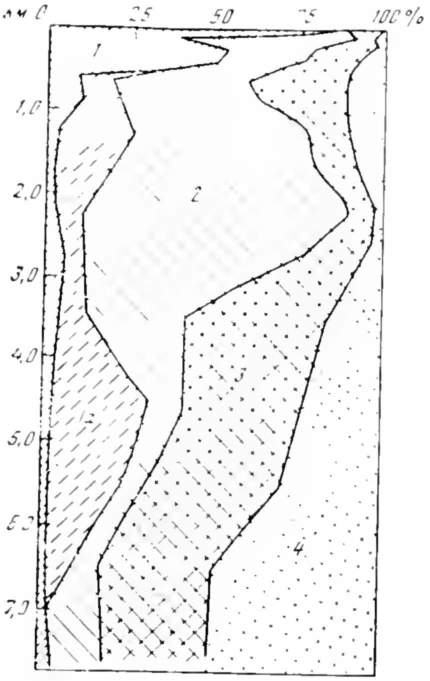


Fig. 4. Change in role of various trophic groups in the plankton of the northwestern Pacific with depth. 1, Filter feeders--phytophages and detritophages; 1a, filter feeder-phytophages which feed in the surface layers and do not feed at the depth where caught; 2, zoophagous species--predators and scavengers; 3, euryphages; 4, radiolaria and their remains and other groups not considered above.

plankton is dominated by euryphages, and only in the benthic layers does a significant quantity of zoophagous polychaetes and amphipods appear, probably associated with the floor.

In contrast to the eutrophic boreal regions, in the oligotrophic tropical regions among the most important group of plankton--the copepods--in the upper 100 meter layer zoophages already predominate, while the significance of filter feeders decreases from 40% in the 0-50 m layer to 15% in the 200-500 m layer. Beginning in the mesopelagic zone, euryphages predominate, continuing to dominate the entire column of water: in the 2000-4000 m layer they make up 76% of the mass of copepods, below 4000 m--94% (Arashkevich, 1972).

In both of the areas in question, the relationship of various trophic groups changes rather similarly as we move vertically downward. However, in the boreal area, predators play a significant role in the plankton down to 3000-4000 m depth, whereas in the tropical area, less rich in food, their role is reduced to nil by a depth of 2000 m. The zoophagous macroplankton is correspondingly distributed: In the boreal waters, a comparatively high concentration of zoophagous forms is observed down to 3000 m, in the tropics--down to 1500-2000 m.

Thus, based on the relationship of the various trophic groups in the pelagic zone, we can distinguish rather clearly different layers, approximately corresponding to the surface, moderately deep and abyssal distribution of the planktonic biomass (Vinogradov, 1968). The superficial layer extends down to 100 (or 200) m and is characterized by clear domination or predominance of filter-phytophages. Then, from 200-500

(750) m is an intermediate layer without clear domination of representatives of any one feeding group. At depths from 750-1000 m to 3000 m in the tropics, zoophages play a significant, usually dominant, role. Deeper, euryphages dominate.

Basic trophic complexes of macroplankton and nekton at various depths. The vertical zones of the oceanic pelagic zone correspond to the trophic complexes of macroplanktonic and nektonic organisms occupying the higher levels of the food chain (Parin, 1970, 1971; Borodulina, 1974).

The epipelagic complex consists of (holoepipelagic) crustaceans, constantly inhabiting this biotope (euphausiids, less frequently shrimp), cephalopods, fish, sea snakes and chelonia and many whales, as well as the interzonal animals which rise to the surface at night to feed (nycto-epipelagic species). The second level predator niche here is occupied primarily by macroplanktonic organisms and relatively small fish (in the higher latitudes, until recently baleen whales were extremely important); at higher levels, only nekton are represented (large fish, dolphins, etc.).

An independent trophic complex can be distinguished in the tropical area in the boundary layer between the epipelagic and mesopelagic zone, at a depth of 100-300 m. This complex combines second and third level planktophages, constantly present at these depths (certain euphausiids and hyperiids, juvenile squids and fish, mature fish from the families Sternoptychidae, Scopelarchidae, etc.) or numerous euphausiids, shrimp and myctophids, migrating here at night from the mesopelagic zone to feed. All these animals, including the interzonal migrants, serve as food for such nektonic predators as fish from the families Paralepididae, Bramidae, Gempylidae and a number of species of squid from the families Ommastrephidae and Onychoteuthidae, which are themselves eaten by the alepisaurs, large ("level") tuna and marlins, sharks and bottlenose whales (but not the sperm whale). All of these, except for the alepisaurs, are genetically related to the epipelagic area (which is indicated in particular by the fact that smaller species of tuna and the juveniles of larger tuna and marlins inhabit the surface levels), and their departure from the upper layers is energetically justified by the richer food available in the boundary area between the epipelagic and mesopelagic biotopes. The epipelagic and interzonal organisms rarely form a part of the food of these predators (Fig. 5), since they feed in this layer during the daylight.

In the mesopelagic zone itself, coexist two trophic complexes--the stable complex, consisting of nonmigrating or short-range migrating animals, and the migrating ("stratal") complex, including organisms which perform daily vertical movements as a part of the migrating sonic scattering layers (SSL). Both complexes consist primarily of macroplanktonic (or micronektonic) crustaceans, cephalopods and fish, primarily third or fourth level predators; the true nektons are very scarce in the mesopelagic zone, the most important of them being the sperm whales, which feed in this layer.

The special trophic complexes of the deep layers of the oceanic pelagic zone--the bathypelagic and abyssopelagic zones--are combined by their

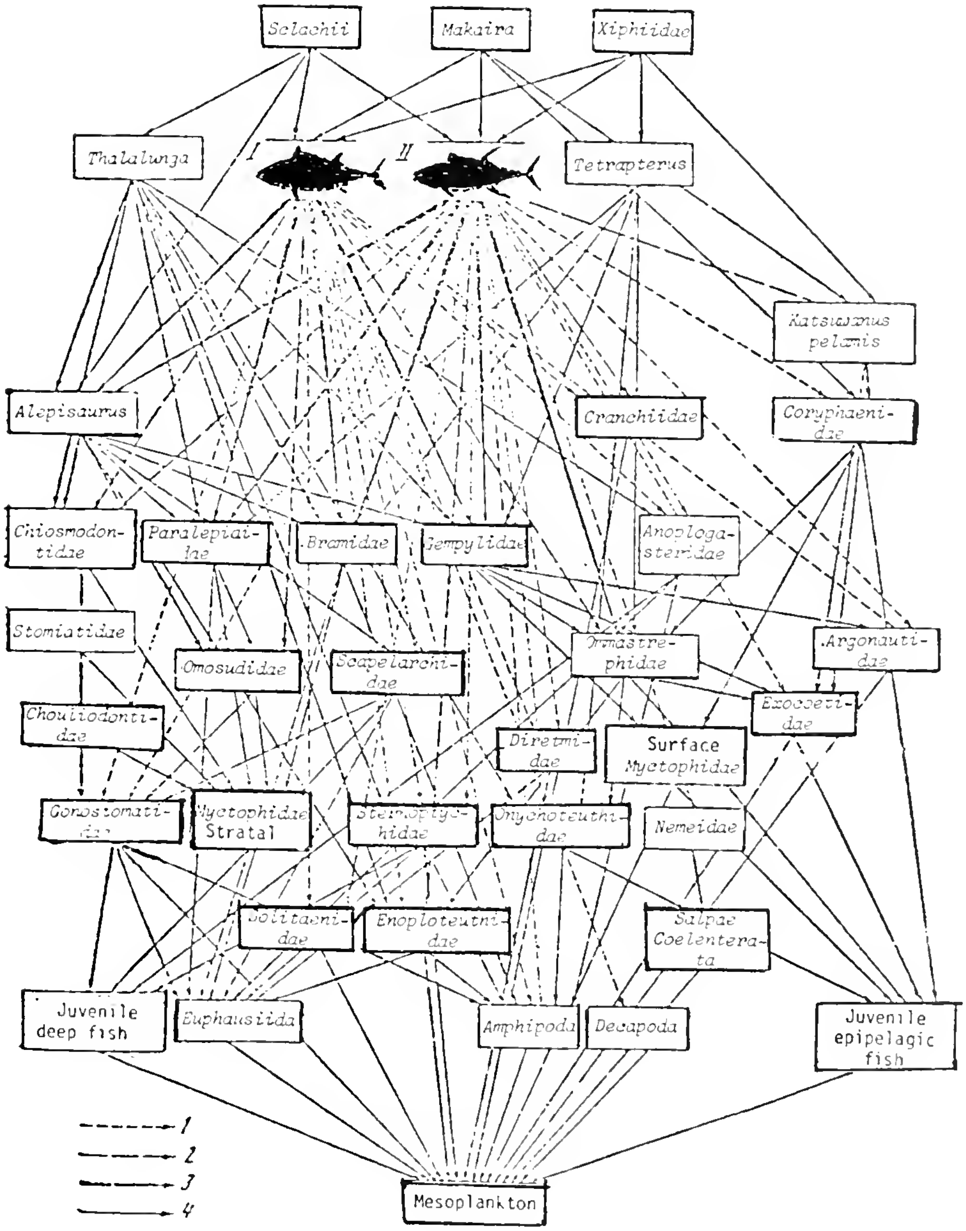


Fig. 5. Primary trophic connections of macroplankton and nekton in the tropic oceanic pelagic zone, on the example of the diet of the bluefin (1) and yellowfin (2) tunas: 1-3, food connections of the tunas: 1, most important (>10% of arbitrary re-established weight of diet); 2, less important (5-10%); 3, still less important (<5%); 4, food connections with other nektonic and macroplanktonic organisms (according to Borodulina, 1974).

adaptation to the scarce food resources of these zones. The animals which make them up have characteristically adapted to reduced energy expenditures, manifested as a transition to a passive mode of life. For this reason, there are no nektonic animals in the bathypelagic or, particularly, the abyssopelagic zone, and even the largest inhabitants of these biotopes--and some fish (the angler fishes *Himantolophus* and *Ceratias*) and squids (*Mesonychoteuthis*) reach a meter or more in length--must be considered macroplankton.

The primary trophic complexes of the macroplanktonic and nektonic animals in the pelagic zone of the ocean, though they are clearly separated, are still interconnected to some extent and form only individual sections of the single trophic network. The "contact" is particularly clearly seen in the complex at the upper boundary of the primary thermocline, where elements of the epipelagic and mesopelagic complexes come in contact and conditions are created for a significant concentration of food resources for the large nektonic predators.

2. Communities of the Arctic Waters.

(E. A. Zelickman)

The cyclical nature of the functioning, i.e., the presence of population waves in the Arctic ecosystem, is a general property of this system, reflected in the formation of all production characteristics. It results from the light limitation of photosynthesis. In an ecosystem which must function in a fluctuating mode, selection fixes only those hereditary changes in organisms which correspond to a broad reaction norm. Compensatory paths of stabilizing selection are primarily limited to multiplication (Shmal'gauzen, 1968). With a brief season of abundant food, selection goes to higher fertility, and selective elimination may be directed toward various phases of ontogenesis. In this case, the reproductive potential of the species, as a rule, which is not realized in the Arctic community, may manifest itself as compensation. Therefore, in the Arctic community, only "opportunistic species" with high ecologic valence: high numbers of population, flexible reaction to unfavorable changes in the environment, high growth rate of the population under favorable conditions and high mortality, can blossom. The dominant species of this profile in the Arctic community can be compared (Margalef, 1968) to a thermostat, consuming a great deal of energy while acting as a regulator. This type of "equipment" withstands extreme conditions, converting fluctuations in the environment to the benefit of the system. Just what are the means of this damping?

If the production of plankton communities is interpreted (Cushing, 1959a, b, 1969) as a result of contradictory relationships among populations, the course of the curve of creation of products is determined by the time interval between the peak of blooming of the phytoplankton and the moment of greatest intensity of consumption. Arctic and boreal communities differ essentially only in the length of this interval, proportional to the distance from the Pole. In other words, an Arctic community as a whole has its own unique "system time," and in each season the community must adapt to this system time, synchronizing its state with the time. The balance between producents and consumers in this interpretation is a characteristic which is more temporal than quantitative. Therefore, the synchronization of the processes of creation of biomass and its destruction at the next trophic level is one of the leading trends in selection in the Arctic ecosystem. Idioadaptation at the species level should support temporal contact and the normal sequence of the cycles, while the equilibrium between production and consumption is checked by the entire system of mechanisms inherent in the community as a whole. One of the indirect mechanisms synchronizing the system is the high P/B coefficient (for values of indicators, see Kamshilov, 1955, 1958; Timokhina, 1968, 1972), corresponding to the seasonal asymmetry of the curve of food resources.

The obligatory pulsation in the status of the community may be a specific method of stabilization of the system, but not a method of its disruption. The fluctuation processes in the Arctic encompass the entire hierarchy of trophic levels in a definite sequence, but with varying intensity. However, in the annual cycle, the production of the community remains relatively stable, since its basic parameters (species composition, numbers, biomass) do not go beyond a certain framework.

The population waves, as an attribute of all life cycles in the Arctic, facilitate the appearance of new genotypes in the evolutionary arena (Huxley, 1942). The fluctuating mode also influences the boundaries of the area of distribution of Arctic and Arctic-boreal species, which alter their "case" with periodic changes of abiotic conditions.

The oscillating type of dynamics predetermines the resiliency of the structure of the populations and the strong intraspecies mutual dependence. The Arctic ecosystem, which is self-reproducing in the oscillating mode, to some extent refutes the thesis of the incompatibility of maximum productivity of a community with the status of its highest stability. If we look upon constancy of relationships of biomass of species in a community as one criterion of stability, this constancy is retained on the average over the annual cycle (see below). Obviously, it is more correct to evaluate, in this case, oscillations in numbers as a manifestation of stability (Preston, 1969): They make the community less vulnerable. From the standpoint of evolutionary advantages, this form of stability can be considered most adequate for biological progress, as understood by A. N. Severtsov.

2.1. Comparison of the Arctic Ecosystem with Other Productive Systems

The concept of "system time" allows us to note the deep structural and functional similarity between the ecosystems of the different productive zones and their particular blocks. For example, the "behavior" of marine and fresh-water Arctic communities is similar (Dodson, 1975; Tash, Armitage, 1967).

The shelf-neritic communities of various latitudes, like the Arctic community, are the arenas of seasonal "demographic explosions." The spatial distribution of phytophages and predators in the area of the polar fronts of the Norwegian and Greenland seas (Gruzov, 1963; Pavshtiks, 1972) is similar to that in the region of the West African upwelling (Bainbridge, 1972): In both cases at the "line" of the front and in the zone of maximum upwelling, phytophages predominate, with predators predominating around the periphery. There are also analogies in the systems of adaptations. We need but recall the similarity of the life cycles and life forms of Arctic-boreal and neritic euphausiids as a counterweight to the oceanic forms, regardless of their latitudinal distribution (Zelickman, 1968a; Gilfillan, 1972). Convergent adaptations are seen in the upper boreal *Calanus finmarchicus* and lower boreal *C. carinatus*, e.g., the winter descent of the stage V copepodites (Bainbridge, 1972).

The small variety of life forms in the Arctic ecosystem is compensated for by the intensive intraspecies divergences. Within the framework of the Arctic ecosystem, sympatric radiation occurs among the dominating species *Calanus*, *Pseudocalanus*, *Limnocalanus*, *Oithona*, *Parathemisto*, *Mysis* and

Thysanoessa. The great number of microzooplanktonic predators, along with the phytophages and the great specific weight of carnivorous feeding, are characteristic for the epiplankton of all productive zones. For example, in the neritic waters of the Barents Sea, in the upper 30 centimeter layer, an asymmetrical quantity of Oithona, Sagitta and Pseudocalanus of all ages is observed, as well as Cladocera, Fritillaria and Oicopleura (Shuvalov et al., 1974). According to our observations, the number of these animals in May-September (per unit volume) in the 0-30 cm layer is 3-4 orders of magnitude greater than in the 0-10 m layer. This concentration of predators and phytophages in the narrow surface layer indicates the precise feeding differentiation of the massive species.

Although in the Arctic community, the biomass of zooplankton in the tremendous water area of the neritic and shelf regions is also higher than in the oceanic waters, the "neritic underutilized phytoplankton," of which A. K. Heinrich wrote (1961a, b, 1962), apparently does not exist. In the Barents Sea, it is in these neritic waters that phytoplankton is consumed earliest and most completely (Roukhiyaynen, 1960). Were this underutilization real, the dominant phytophages would not eat animal food, either in winter or, particularly, in the summer. In nature, Calanus finmarchicus supplements its protein supply by predation, both summer and winter (Adams, Steele, 1966), although in the laboratory, this species can survive for long periods of time on a diet of algae alone. On the shelf of the epicontinental seas of the Arctic, for example near Novaya Zemlya (Zelickman, Golovkin, 1972), the great biomass of zooplankton is formed where the phytoplankton is richest. The excess phytoplankton, i.e., imbalance, is nonexistent: The disproportion which arises is eliminated by changes in the population of the massive species and in the number of their generations. In other words, the temporary "excess" is regulated by the consumers themselves. Thus, with low concentrations of algae cells, the rate of filtration of the Copepoda decreases, and the level of nutrition supports only the minimum vital activity. The low rate of consumption allows the phytoplankton to increase in number, after which it is immediately utilized by the Copepoda to increase their own egg production (Adams, Steele, 1966; Poulet, 1974).

2.2. Spatial and Morphophysiologic Differentiation of Organisms as a Form of Transformation of Fluctuations within the Arctic Ecosystem

The flexibility, "elasticity" of the system, given the relatively low number of life forms, is achieved, particularly, by redistribution of "energy clusters" within the community both in time and in space. The space and time segregation of massive species and their hemipopulations is clearly expressed. The capability of organisms to hold themselves in a predetermined water mass reinforces this heterogeneity, guaranteeing the species and their hemipopulations synchronous coexistence. During the polar day, the intrapopulation spatial differentiation is primarily expressed in the horizontal plane. One example can be found in the local schools and zones of abundance of C. finmarchicus, Thysanoessa inermis, and T. raschii (Zelickman, 1958, 1961b). In the Barents Sea, the main body of zone of abundance of Calanus, Pseudocalanus and euphausiids, as well as their young in spite of seasonal movements, are always distributed throughout the depths. The euphausiids of the present and previous year are distributed horizontally.

The role of ontogenetic migrations in the formation of spatial heterogeneity under the conditions of the Arctic ecosystem increases due to the interruption (or decrease in the amplitude) of diurnal vertical migrations during the polar day. It is the ontogenetic descent which determines the replacement of the spring and summer oceanic complex of species by the summer and fall neritic complex, changing the nature of the plankton diet of the fish. In many cases, the ontogenetic migrations also result in temporary intraspecies segregation. For example, in Calanus glacialis in the fjords of Greenland (McLellan, 1967), the rise of VI copepodites to the surface is synchronized with the phytoplankton peak in the internal and external areas of the fjords, so that the stage I copepodites are universally supplied with food. Therefore, the males with spermatophores do not appear simultaneously in the various subpopulations.

There are various means of achieving spatial separation. One of these is the aggregation of distribution observed in any community. When there is a very high numerical strength of species, particularly in a glacial-neritic system, clear effects of aggregation are observed. In the shallow Arctic bays (e.g., in the Cheshskaya Bay of the Barents Sea), a multitude of ephemeral "microcommunities" are observed. They are rather permanently isolated from each other due to the shallow turbulent currents and complex density stratification. Over a distance of a half mile, the plankton might differ by 5 or 6 orders of magnitude as to number, as well as faunistic composition. The number of crustaceans in accumulations might reach tens of thousands of individuals per cubic meter (Zelickman, 1968a).

However, the general trend in "demographic strategy" in the Arctic ecosystem is survival through unfavorable conditions and awaiting more favorable conditions, achieved in many ways. Survival adaptations include, for example, latent stages of development in animals (N. M. Pertsova, 1974; Prygunkova, 1974; Zelickman, 1972) and the quiescent spores of algae; the presence of the latter is one factor causing the first climax in the development of phytoplankton to be observed in the shoals and air holes.

Ecologic differentiation and "waiting strategies" are also supported by temperature regulation. During the vegetation season, the temperature changes over broad limits, making the development of species of various biogeographic and ecologic complexes possible. The differences in the peaks in numbers are related to temperature as one of the background mechanisms regulating the coexistence of the species. The temperature determines the time of development of the eggs of the Copepoda (N. M. Pertsova, 1974; McLaren, 1965; Corkett, McLaren, 1970; Corkett, 1972). The larger the eggs, the longer their development. Considering the differences in diameter of the eggs of the various species (C. finmarchicus--145 μm, C. helgolandicus--163 μm; C. glacialis--178 μm; C. hyperboreus--190 μm), it becomes understandable that in zones where the areas of distribution of these species overlap, the appearance of the young does not occur at the same time and, consequently, the maximum in numbers is not reached simultaneously. Furthermore, there is reason to believe that the acclimation of females which survive the winter to low temperatures facilitates more rapid development of their eggs (Landry, 1975) and, consequently, separate utilization of the plant resources in the spring and summer generations of Copepoda. The temperature plasticity of the eggs of the Copepoda is tremendous (Corkett, McLaren, 1970), which, in addition to the relative eurybiontity of mature individuals, makes the disappearance of any species during a single annual cycle in any actual natural situation impossible.

The regulatory mechanisms guaranteeing the maximum enrichment of the population during the short period of abundant food also include the seasonal change in the relationship of the sexes. In the winter, females predominate among the sexually mature Copepoda, the fraction of males falling possibly as low as a few thousandths of one percent. The number of males increases as the mating season approaches, at which time they rapidly metamorphize from the fourth stage. Another reserve for optimization of numbers lies in the variability of the number of eggs (McLaren, 1966; Corkett, McLaren, 1970). It is manifested as seasonal variation of the number of eggs in the laying and, depending on the number and size of layings, on the current and previous degree of nutrition of the crustaceans. A decrease in fertility due to a shortage of food for the Copepoda is thus reversible. If the deficiency lasts longer, the fertility is decreased for a long period of time, thus decreasing the nonselective elimination. Selection by change of the fertility norm touches not only upon the phase of egg production, but all of ontogenesis. If the population density of *Cyclops* is too high, the number of females laying fertilized eggs decreases, while the period of postembryonal development increases (A. L. Zelickman, 1946; A. L. Zelickman, Heinrich, 1959). The lower the population density (greater the supply of food), the more closely spaced the emergence of the nauplii and the higher their survival rate. This is possibly one means by which the minimal wintering number of Copepoda after a year of low productivity provides a tremendous population peak during the next spring cycle (Zelickman, 1960b; Zelickman, Kamshilov, 1960). It cannot be excluded that when population density is low, exocrine regulation of the numbers is eliminated.

However, for benthic and interzonal species of Copepoda in the Arctic community, other adaptations are characteristic, similar to those of the deep-sea pelagic species, the conditions of existence of which are more stable (Matthews, 1964; Vinogradov, 1968). It is characteristic for them that there are no sharp fluctuations in number (*Chiridius armatus*, *Bradyidius bradyi*, *Aetideus armatus*, *Xanthocalanus minor*, etc.); the number of eggs (falling to the bottom) is less than that of the epipelagic species; the number of layings per year is less; the high amount of vitellus in the eggs, and, correspondingly, the lecithotrophy of the nauplii; a decrease in the number of nauplial stages; year-round fertilization of females; longer duration of the fifth copepodite stage. In the community, these species "collect the trash," and the period of their relative abundance coincides with the phase of summer decrease of zooplankton in the upper layer. The temperature regulates the sequence of breeding of the benthic species and allows them to be spread in terms of times of the beginning of breeding, providing their progeny with relative regularity of food supply. In the interzonal dominant species in the high Arctic waters (*C. glacialis*, *C. hyperboreus*, *Pareuchaeta* spp., *Metridia longa*), adaptations are in part similar to those mentioned above; the copepodites live a long time and are capable of fasting for long periods, expending the high-calorie fat and waxy esthers. An increase in the concentration of waxy esthers gives the Copepoda neutral buoyancy, compensating for the loss of energy during the longer active swimming stage. For these forms, as for deep-sea species, food specialization is characteristically slight, with a higher share of detritus in the diet and the ability to change methods of feeding, trapping all potential food when its concentration is low (Vinogradov, 1968; Mullin, 1963; Mauchline, 1966; Poulet, 1973, 1974). The food spectrum is particularly broad among the eurytopic species which inhabit the oligotrophic water areas. For example, Mysis relicta in the summer feed on detritus, phyto- and zooplankton, while in the fall, with the beginning of the regular vertical migrations, they eat only Cladocera; Metridia longa in the summer is primarily a phyto-planktophage, in the winter feeding on the young of the Copepoda (Lasenby, Langford, 1973; Haq, 1967). The same features of nonselectivity are inherent in the epiplankton filter feeders Fritillaria and Oikopleura (Madin, 1974). The neritic Temora longicornis and Centropages hamatus can also eat the spores of the Phaeocystis, formerly considered inedible (Jones, Haq, 1963). Omnivorous tendencies increase in the higher latitudes, both in predators such as the polychaete Tomopteris septentrionalis or the copepod Pareuchaeta norvegica, the number of which is relatively stable (Kielhorn, 1952; R. Williams, 1974; Dodson, 1975), and in phytophages. C. hyperboreus may form a surface and deep-water population in the same location, the deep-water population being distinguished by a high level of consumption of microzooplankton. C. helgolandicus may winter exclusively by carnivorous eating (Corner et al., 1974), and C. hyperboreus normally forms eggs on a diet of "meat" (Lee, 1974). The utilization of animal food by plankters generally increases when food concentrations are low (Gaudy, 1974).

The time factor is extremely important for the trophics of the Arctic community. Bacterial mineralization and the decay of dead tissue occur more slowly in cold water (Harding, 1973), which preserves a larger supply of food for second-order consumers. The breeding of a number of invertebrate species in the autumn and winter allows the resources of food to extend throughout the year. The basis of the biomass of the Arctic community is created by populations of relatively large, slowly growing organisms with slow metabolism. This also is facilitated by the great length of life cycles (1-2, sometimes even 3 years) of Parathemisto, Sagitta, Thysanoessa, etc. In the boreal waters, these animals have shorter cycles (Bogorov, 1940; McLaren, 1966, etc.).

2.3. The Seasonal Course of the Process of Production in the Arctic Community

Let us briefly study the actual picture of production, basically on the example of the Barents Sea, which is included entirely in the Arctic basin. Its plankton population is representative for the Arctic community. It is also important that the Barents Sea is an epicontinental body of water, while a huge shelf zone is typical for the Arctic.

The fluctuations in annual quantity and prevernal reserve of biogens observed in Arctic waters depend primarily on the intensity of the vital activity of the plankton. The vernal development of phytoplankton, in any case in the Barents Sea, is not limited by the reserve of biogens. For example, in 1958, with the minimal winter reserve of nitrate nitrogen observed in 1949-1959, a maximal brood of phytoplankton was observed. The development of phytoplankton begins at minimal temperature and maximum vertical stability of the euphotic layer. However, by summer the reserve of biogens is exhausted, and the shortage begins to inhibit the development of phytoplankton. Only in regions of abundant bird population, due to the local enrichment of the littoral waters with biogens, does stable production of bacterio- and phytoplankton continue throughout the entire spring and summer (Golovkin, Zelickman, 1965; Zelickman, Golovkin, 1972).

The greatest May peak in development of phytoplankton is that of Phaeocystis; the April and July peaks formed by the diatoms partially merge with it; the development of the peridinia is significant in June and September. The greatest maximum is that of Phaeocystis pouchetii: over 7.8 billion cl/m^3 (Roukhiyaynen, 1960), while the scale of the April-May peak of diatoms is less: over 800 million cl/m^3 in the 0-50 m level. The most productive waters in the spring are the Arctic and mixed waters. In the summer, the oceanic complex of phytoplankton is replaced by a neritic complex.

The Calanus and euphausiids, which make up the basis of the winter biomass of zooplankton, spend October through February at depths of over 150 m. The locus of the winter benthic concentrations of crustaceans and, correspondingly, the locus of their March-April rise, forces us to think that the basis of the Barents-Sea superpopulation of these species is the indigenous population. This is confirmed by morphometric analysis of the stages of development (Zelickman, 1958, 1968; Zelickman, Golovkin, 1972; Nesmelova, 1966, 1968). In the Barents Sea, in any case to the east of the meridian of the Kola (33°30'E), over 70% of the population of plankton in the Arctic, local and neritic waters, consists of the autochthonous population.

With respect to time, the first consumers of the phytoplankton are the nauplii of the barnacles. Reproduction of the barnacles heralds the beginning of the biologic spring in the Arctic community. The number of Balanus nauplii appearing on the southeast shore of the Barents Sea, usually by the 20th of March, increases within a period of a few days to $40\text{-}50 \cdot 10^3$ per cubic meter in the 0-10 m layer. The reproduction of the Balanus is independent of water temperature. The metamorphosis of the second nauplial stage into the third, the intensive consumer of phytoplankton, coincides with the increase in the number of diatoms. The barnacles "can wait for" the appearance of suitable conditions for reproduction; embryos which have completed their development sometimes wait for 12-18 days in their capsules before the appearance of the nauplii in plankton. The barnacles precede the spawning of the other massive species, which allows the larvae to avoid competition during the most vulnerable stages of ontogenesis.

The beginning of breeding of the *Calanus* and euphausiids and the rise of the biomass (Fig. 6) coincide with the beginning of blooming of phytoplankton and is also unrelated to the absolute temperature index (Zelickman, 1958; Kamshilov, 1952, 1955). Since the spermatophores of the male of *Calanus* and euphausiids are formed long before the spring rising of animals to the surface water, it is possible that spawning occurs only after a certain period which the mature individuals must spend in the light. Breeding may occur over a broad temperature range, approximately identical for all the mass species: for *Thysanoessa raschii*, from -1 C to 7-10 C, for *T. inermis*, from 0-7-10 C, for *Calanus*, from -1 to 11 C. The prespawning concentrations of euphaisiids and *Calanus* are formed in the euphotic layer, where their young will later feed. The oceanic, primarily predatory, forms (*Thysanoessa longicaudata*, *Pareuchaeta* spp., *Metridia* spp.) are less closely related to the phytoplankton; therefore, their area of breeding is broader and more continuous, their breeding period more extended. The breeding peaks of the three massive phytophages are displaced with respect to time; for example, in the Barents Sea, the *Calanus* breeds in April, *T. inermis* in May, *T. raschii* in June.

Since the phytoplankton bloom begins in various sections of the water masses at different times, naturally an alternation develops in the zones of abundance of the young, then of the mature individuals of the massive species. Therefore, the relative significance in the increase of the biomass of the deep water regions and the shallow-water regions changes by seasons: During the spring-summer season, the biomass of zooplankton is higher in the shallow water during the fall and winter--in the deep-water regions. This process of redistribution of living matter is related to the seasonal ontogenetic migrations and cycles of breeding of the holo- and meroplankton animals (Fig. 7). The neritic waters (in the comparatively productive layer) are richer.

The separation of the zones of large numbers of *Calanus* and young euphausiids in May-June in waters with abundant phytoplankton bloom can be explained not only by the competition for food, but also by exocrine interactions. Generally, direct and indirect trophic and topical interrelations of the dominant species of zooplankton with the nannoplanktonic heterotrophs and with the phytoplankton are very close. Sometimes, these bonds are broken at the final, trophic level, bypassing the previous levels. For example, in the neritic communities of colonial birds, the euphausiids and mysids are eaten in large numbers by thick-billed guillemots and kittiwakes, the *Calanus* by the little auk (Zelickman, 1958; Golovkin et al., 1972). Sometimes, direct expulsion of a species from its ecologic niche is observed, as occurred in 1956 with *Pseudocalanus elongatus*, developing rapidly in Svyatonosskiy Bay of the Barents Sea after grazing of *Calanus finmarchicus* there by the Murmanc herring (Zelickman, 1961a).

The summer maximum of zooplankton is created by *C. finmarchicus*, *Pseudocalanus*, *Oithona*, *Oncaea*, *Fritillaria*, *Oikopleura*, and in August-September--by abundant small hydromeduses and ctenophores. In the shallow

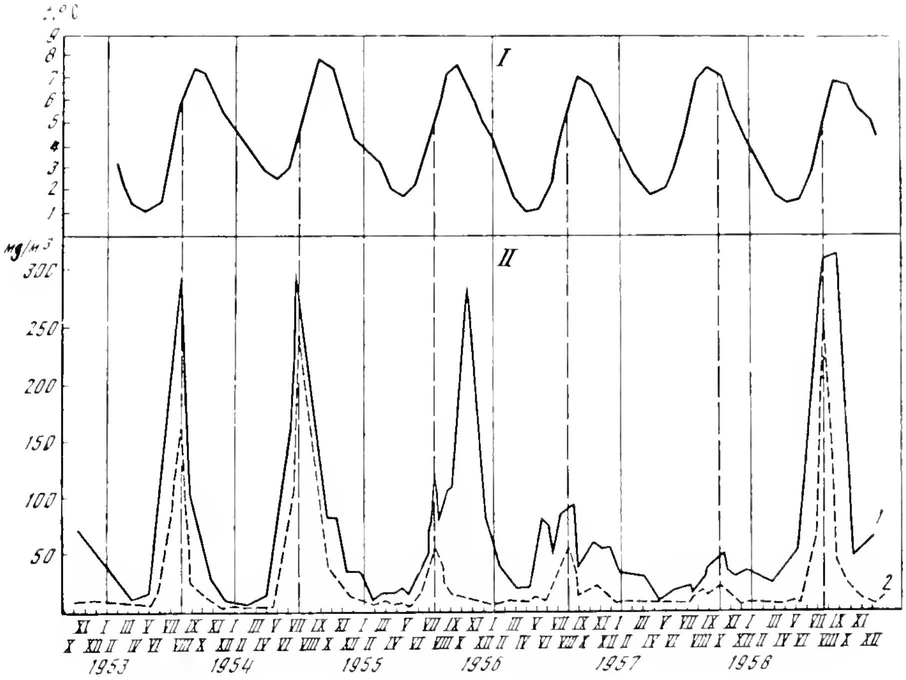
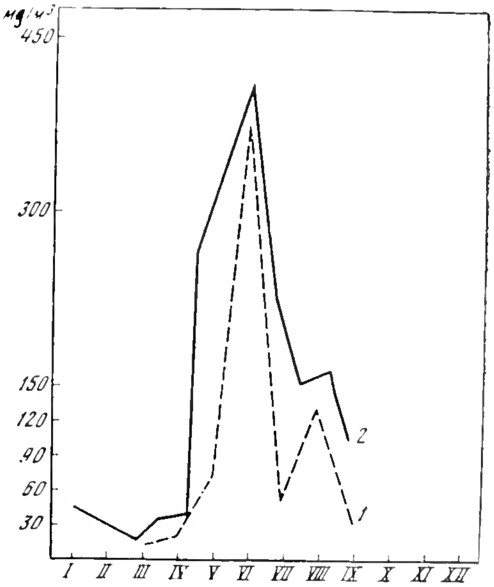


Fig. 6. Perennial dynamics of zooplankton biomass of Barents Sea on the shore at Murman (section through the Dal'nie Zelentsy traverse). I, water temperature, 0-50 m; II, mean monthly biomass throughout the entire column of water, for all plankton (1) and Calanus (2) (Zelickman, Kamshilov, 1960).

Fig. 7. Annual cycle of changes in biomass of plankton of Barents Sea by months (Manteyfel', 1941): Ordinate, mean plankton biomass for 0-100 m level; 1, littoral waters from Ringvassë Island to Svyatoy Nos Cape (1934); 2, southwestern area of open sea (1939).



neritic zone, the dominant species are recruited from the complex specific for this zone: *Acartia longiremis*, *A. clausi*, *A. bifilosa*, *A. tumida*, *Centropages hamatus*, *C. mcmurrichi*, *Temora longicornis*. In estuaries, to these forms we must add *Limnocalanus grimaldii*, *Senecella calanoides*, *Drepanopus bungei*, *Derjuginia tolli*, *Heterocope appendiculata*, *H. borealis*, *Eurytemora hirundoides*, and *E. herdmani*, the Cladocera and the rotifers. The biomass of the estuarian complex may reach 30 g/m^3, but namely its productivity fluctuates from season to season by hundreds and thousands of times.

The most important reason for the seasonal summer-fall decrease in biomass of zooplankton in the Arctic community is consumption by planktonophagous fish, fingerlings of benthic fish, as well as sagittae, medusae and ctenophores. The elimination of the Copepoda by fish occurs in all stages of ontogenesis, with not only phytophages, but also predators involved in the process (Sysoyeva, 1973; Aslanova, 1971). There are a multitude of invertebrate predators: for example, in the southeastern portion of the Barents Sea in July and August, the number of ctenophoran *Bolinopsis infundibulum* reaches 170 per cubic meter, *Pleurobrachia pileus*--30-40 per cubic meter, the medusae *Rathkea*, *Obelia*, *Aglantha digitale*, *Tiaropsis multicirrata*--up to 3000 per cubic meter (Zelickman, 1961a, 1966, 1969). The rate of elimination of the *Calanus* depends directly on the population of *Bolinopsis*: the correlation coefficient between the overall elimination of *Calanus* and the occurrence of ctenophores is 0.93±0.06. In August alone, the Ctenophora may decrease the population of *Calanus* by a factor of 5 (Nesmelova, 1968). The peak of the population of medusae and ctenophores is independent of temperature and is related to the population of prey, occurring usually 2-4 weeks after the peak of Copepoda biomass, regardless of the hydrologic specificity of the year, but the duration of the period of high population of Coelenterata is closely related to the temperature (Zelickman, 1965; Zelickman, 1972). The number of invertebrate predators is in turn regulated by a secondary mechanism--their consumption by more narrowly specialized predators--other ctenophores and meduses. For example, *Beroe cucumis* consumes only *Bolinopsis*. *Tiaropsis multicirrata*, when highly concentrated, after consuming the crustacean zooplankton, begins eating *Rathkea octopunctata*, turns to cannibalism, etc. (Zelickman, 1960b, 1965; Zelickman, Kamshilov, 1960; Zelickman, 1972; Conover, Lalli, 1974).

Let us trace this scale of creation of living matter in the Arctic community, using the Barents Sea as an example. During years with *Calanus* domination, the curve of the dynamics of biomass in the plankton has a single peak (see Fig. 6); as the number of *Calanus* drops, the curve takes on more than one peak and the maxima are shifted in time. The annual production of *Calanus finmarchicus* averages 250-300 mg/m^3, about 90% of the annual production occurring between April and early October (Kamishilov, 1958). The higher the biomass of the *Calanus*, the greater its relative significance in the plankton. It is logical to presume that with full realization of its productive potential, *Calanus* would expel the remaining zooplankton. Extrapolating the curve of relative significance of *Calanus* (Fig. 8) to 99.9%, we obtain the value of the theoretically maximum possible spring-summer biomass of zooplankton (excluding Protozoa, Medusae, Ctenophora and other crustaceans) in the upper 50 m layer is about 3 g/m^3. This level of biomass has actually been observed repeatedly. For example, in June-July

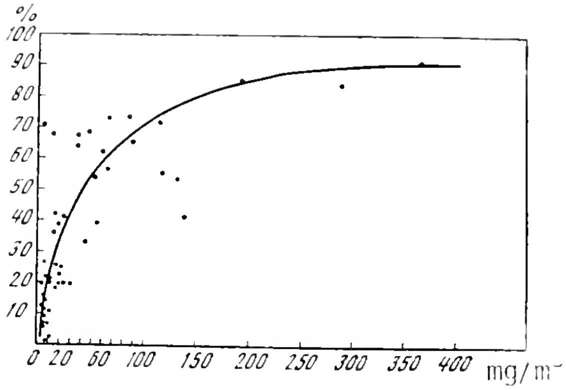


Fig. 8. Variation between absolute (abscissa) and relative (ordinate) values of biomass of Calanus finmarchicus s.l. in the plankton of the Barents Sea (Kamshilov et al., 1958).

of 1975 in the neritic waters of the Barents Sea, the biomass, according to our data, was about 3 g/m^3 in the 0-50 m layer, over 99% of the biomass being Calanus, with other crustaceans practically absent in the plankton.

The remaining members of the community, capable of exceeding the Calanus in number, though not in biomass, such as Oithona, Fritillaria and others, damp the possible excursions of the biomass and of production. The flexibility of the system, its stability in relationship to deformations, increases when other species are present, each of which fails to reach its maximum possible biomass. The "price" of increased stability is incomplete realization of the potential biomass and production, which is a general trend in any pelagic zone community, including the Arctic community, but in the latter it is particularly severe for opportunistic, subordinate species. Since absolute expulsion of "non-Calanus" zooplankton does not occur, it is clear that certain limiting factors are at work, increasing the pressure of the environment on the dominant species. Consequently, even in Calanus, the reproductive potential is not fully realized.

In the Arctic community, as in general in communities with nonrigid hierarchic structure, the species following the dominant species in rank, in case of a decrease in the number of the latter, takes its place. In hydrologically unfavorable years, the total biomass remains at the median level, but the relationship of the dominant groups, primarily in the neritic zone, changes: In the White Sea, for example, the cladoceran take first place in terms of biomass rather than the copepods; in the estuarine Arctic plankton, the most numerous is at times Limnocalanus at times Drepanopus, at times Senecella or the Cladocera.

The maxima in the Arctic plankton population curve may be numerous, up to 7-8 in neritic waters (Fig. 9), with the curve of the annual course of biomass having two, less frequently, three peaks. The course of the curves of the dynamics of the populations of primarily carnivorous plankters is more complex than that of primarily phytophagous plankters (Fig. 9A). The smaller peaks of individual groups late in the year may merge (Fig. 9B). Variations of this type have been traced by many authors for the Barents Sea (Manteyfel', 1939, 1941; Zelickman, Kamshilov, 1960), the Norwegian Sea

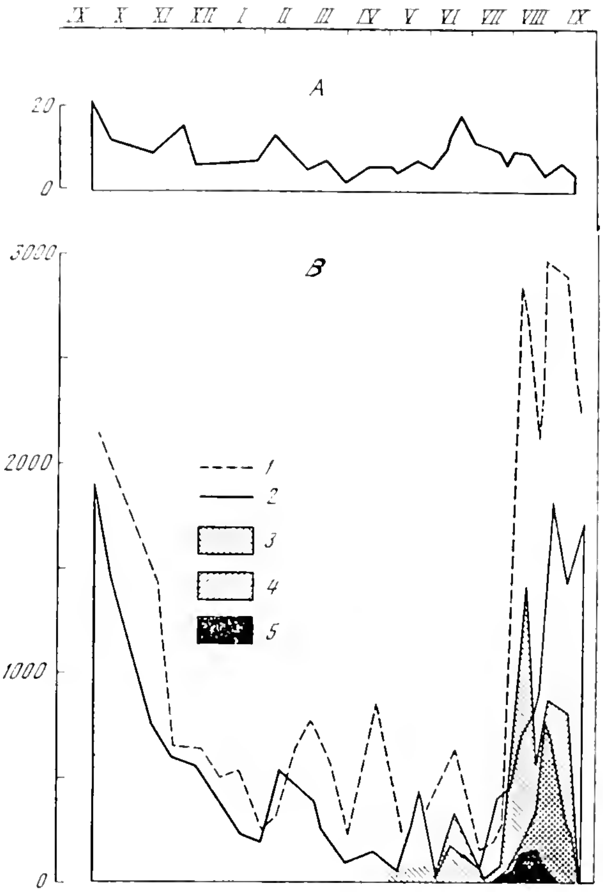


Fig. 9. Annual cycle of changes in population of zooplankton in 1955-1956 at Igloolik (Fury and Hekla Strait, Canadian Arctic) (Grainger, 1959). Ordinate--number of specimens in the 0-50 m layer, abscissa--months; A, mainly predatory; B, mainly phytoplankton; 1, Copepoda, 2, all zooplankton; 3, Copepoda nauplii; 4, Cirripedia nauplii; 5, Polychaeta larvae; 1, 3--0.24 mm mesh size; 2, 4, 5--0.57 mm mesh size.

(Wiborg, 1954), Greenland Sea (Kielhorn, 1952; Digby, 1953; Grainger, 1959; Gruzov, 1963; Pavshtiks, 1972) and the White Sea (Konoplya, Kokin, 1973; Kolosova, 1975). The further north the zone in question, the fewer the number of peaks on the curve, with the meroplanktonic elements of the community disappearing first. In the high Arctic subarea, the generalized characteristics of seasonal development of zooplankton do not differ in principle from those in the low-Arctic subarea (Digby, 1953; Hughes, 1968; Pavshtiks, 1972). Only the absolute biomass and time parameters vary, while the number of peaks decreases.

In the Arctic community, the length of the biologic seasons depends on the latitude. The further north, the more the times of appearance of the spring-summer and summer-fall faunistic complexes come together. In the Arctic, the spring processes of blooming of the water always begin earlier in the neritic water, over shallows and along the ice fields. The seasonal changes in the zooplankton population beneath the continuous ice also occur in the summer, but the number of animals increases but little, and below 250 m remains practically unchanged, less than 1 specimen per cubic meter for each species (Vircetis, 1957; Pavshtiks, 1971a, b; Harding, 1966; Hughes, 1968; Hopkins, 1969). However, the species variety increases, particularly in the lower horizons of the Central Polar Basin, due to the seasonal increase in the influx of Atlantic water with its rich fauna. The predatory and partially predatory forms--*Metridia longa*, *Calanus glacialis*, *C. hyperboreus*, *Pareuchaeta* spp., large sagittae, mature medusae *Aglantha* and *Cyanea*, Ctenophora, Amphipoda--are present in small quantities throughout the year. The growth of biomass in the 0-50 m layer in the high-Arctic zone at first also occurs due to rising of the animals from the depths, then due to their breeding and growth. The number of small predators--*Oithona similis* and *Oncaea borealis*--increases in the summer. The *Calanus* and *Oithona* may represent 95-99% of the total number of plankters. The number of *Calanus* increases beginning in mid-May, decreasing in September, after which the number of small Copepoda increases. The population peak of the relatively larger meduses and ctenophores occurs in April-May, of the smaller forms--in July-August, synchronously with the Appendicularia. The fraction of predators in high-Arctic waters is high: The number of mature large predators is only one or two orders of magnitude less than the number of *Calanuses*. The total biomass, from 20 mg/m^3 in late March, increases to 250 in the second half of April-May and 400 in August, dropping to 200 in late September and then rapidly decreasing to the winter values (data for the northern area of the greenland Sea). The winter stock inhabits the lower layer, dropping to depths of over 1000 m. The various species descend at different times. The *Metridia*, *Microcalanus*, *Pareuchaeta*, and *Spiratella* breed in the winter. In zones with intensive horizontal movement of masses of water (e.g., Scoresby Sound), the indigenous plankton reaches only 13% of its summer population maximum (Digby, 1953). In the epicontinental seas and on the shelf, the vernal maximum consists more than 70-80% of indigenous populations.

2.4. Perennial Changes in the Biomass of Zooplankton of the Arctic Pelagic Zone

The productivity of the Arctic community is a resultant quantity from a complex net of biotic relationships, functioning against the background of cyclic changes in abiotic factors. Both the deep-sea and the shelf and neritic water areas represent quasi-stable fields of production with definite gradients in space and time, preserved from year to year and generally independent in the temperature aspect. Thus, in the Norwegian Sea in 1959-1963, the mean annual values of biomass and production of zooplankton for the sea as a whole differed from year to year by a factor of not over 2 (Timokhina, 1968, 1972). In the Barents Sea in 1934-1939, the mean annual indicators were approximately the same (Yashnov, 1940). The production is invariably highest in the Arctic and shore waters (averaging 55 t/km^2) and lowest in the warm Atlantic waters (averaging 9 t/km^2). The maxima of production and biomass of the dominant species occur in various water masses, or diverged vertically or horizontally through a single mass of water (Zelickman, Kamshilov, 1960; Zelickman, Golovkin, 1972; Timokhina, 1968).

An analysis of a representative series of 22 years of almost monthly plankton samples collected by a Longhurst-Hardy automatic plankton sampler at a depth of 10 m in the north Atlantic showed no clear connection between climatic changes and seasonal fluctuations in the abundance of zooplankton. It showed only that various species or groups of species have varying tendencies of changes in their number within and between years (Colebrook, 1972a, b). The greatest limits of variability in numbers are seen as we compare different species; the differences are significantly less when we compare plankton as a whole for different months, least of all when we compare different years (Colebrook, 1972a, b). The number of Copepoda before the beginning of the spring development differed in different years by a factor of less than 2, regardless of the preceding and subsequent peaks. The times of appearance of the maxima in the numbers of Copepoda, the duration of the peaks and the scale of the second, usually smaller, maximum were more variable.

Of particular interest for a general description of the ecosystem is the slight variability of annual production indicators (Table 2).

This variability from year to year is somewhat greater in the shallow southeastern area of the Barents Sea (Table 3), where the significance of invertebrate predators is somewhat greater, decreasing the summer-autumn biomass to 1/4-1/5 of the previous level (Nesmelova, 1968; Zelickman, 1961c).

The relative constancy in the values of production is maintained by various mechanisms which standardize the population, acting primarily on the early stages of ontogenesis. For example, the relative constancy of the number of *Calanus* nauplii indicates constancy of the number of breeding females, capable of maintaining the initial numerical level of nauplii. The number of *Calanus* nauplii in a cross section through the Kola meridian in May (Degtyareva, 1972) is given below:

Year	1959	1960	1961	1962	1963	1965	1969
Specimens/m^3	1103	1011	1019	1130	297	1101	1651

In 40 years of studies of plankton of the Barents Sea, samples were taken during periods of cooling and warming of the Arctic, covering various stages of activity of the fishing industry, changing the plankton consumers. Therefore, it is useful to look at a few more figures. In the southwestern Barents Sea during the warming trend (1929-1937), the biomass of zooplankton in the 0-50 m layer averaged 5-15 mg/m^3 in December-March, 100-200 mg/m^3 in April, 500-900 mg/m^3 in June, with the individual maximums rising to 5000 mg/m^3 (Manteyfel', 1939, 1941; Yashnov, 1939, 1940). It remained approximately the same in 1954-1969, which saw both very warm and very cold years. In the southeastern portion of the Norwegian Sea, the biomass was the same during warm (1927-1939) and cold (1949-1951) years (Wiborg, 1954). Along the shores of Spitsbergen in 1959-1966, the seasonal and annual total volume of plankton in the 0-25 m layer varied by approximately an order of

Table 2. Biomass of plankton in 0-50 m layer (mg/m^3) in southwestern part of the Barents Sea in different years (Degtyareva, 1973 and personal report).

Season	1959	1960	1961	1962	1963	1964	1965	1966	1968	1969	1970	1971	1972	1973	Mean for all years
April-May	118	230	159	129	95	81	79	156	125	138	79	137	137	212	129
June-July	416	417	303	310	308	282	500	384	407	421	319	448	515	525	394

Table 3. Mean annual and mean maximal values of zooplankton biomass (mg/m^3) through entire thickness of water in the southeastern part of the Barents Sea (Zelickman, Kamshilov, 1960, modified).

Biomass	1951	1952	1953	1954	1955	1956	1957	1958
Mean annual	100	23	45	129	71	67	60	48
Mean maximal	-	-	287	300	291	93	45	337

magnitude (Lie, 1968b), while fluctuations in the 100-600 m layer did not exceed 0.05 ml/m^3 (Lie, 1968b). The number of mature euphausiids of Thysanoessa inermis and T. raschii (by trawl net collections) in the Barents Sea in 1954-19752 varied by a factor of 3-4 (Drobysheva, Soboleva, 1976). Five-year annual collections in Chupa Bay (White Sea) showed that the zooplankton population in the 0-60 m layer was approximately 10 times as numerous in July as in January, the biomass being about 4-5 times greater (Prygunkova, 1974).

The data presented above indicate that zooplankton of the Arctic community, in spite of significant perturbations in climate and the hundred-year pressure of anthropogenic factors, has retained a rather stable mean level of production, indicating clear homeostasis of the system. Consequently, Arctic plankton can withstand significant stress, while retaining its stability and integrity. The matter is quite different with the nekton. As a result of fishing, the economically valuable species which previously predominated have greatly decreased in number, their niches being immediately occupied by other plankton consumers, less valuable from the human point of view. Thus, the herring have been replaced by poutassou, the feeding areas of the cod, pollock and haddock have been partially occupied by the Arctic cod and capelin (Sonina, 1969, 1973; Ponomarenko, 1968). The zooplankton population can drop irreversibly only in response to very basic changes in the substratum (e.g., an increase in pollution) and (or) human interference in the interrelationships of the basic units of the ecosystem.

3. Communities of the Temperate Waters of the Northern Hemisphere

(S. A. Mileikovsky, L. A. Ponomareva, T. N. Semenova)

3.1. Some Biological Peculiarities of Planktonic Communities in the Cold-Temperate Regions of the Northern Hemisphere

V. G. Bogorov (1941, 1974) worked out a scheme of biologic seasonal cycle in the plankton of the temperate waters of the northern hemisphere, describing its annual cycle as bicyclic with four phenologic (biologic) seasons. During biologic winter, the annual minimum of plankton occurs with predominance of zooplankton over phytoplankton. The biologic spring is the time of the annual maximum of plankton biomass, with significant predominance of phytoplankton. In the summer, the zooplankton reaches its maximum, while the total biomass of plankton decreases, and the biomass of phytoplankton becomes equal to or less than the biomass of zooplankton. At the end of the summer and in the fall, a second, smaller maximum of phytoplankton develops, and at the end of the fall it begins to decrease, leading to the winter minimum. During the course of the annual cycle, the development of phytoplankton precedes that of zooplankton, the difference between the maxima and minima of phytoplankton being greater than is the case for the zooplankton.

The scheme of V. G. Bogorov, however, was constructed practically completely on materials observed in the North Atlantic. A. K. Heinrich (1961a) developed the scheme further and made it much more specific by considering the extensive material available concerning the North Pacific. She showed that the annual cycles of the various species of zooplankton are too different to allow any biologic season in the plankton to be described only by specific age composition of the whole zooplankton. Similarly, we cannot find identical characteristics of analogous seasons in terms of the relationship between the quantities of phytoplankton and zooplankton for all regions in the temperate latitudes. Therefore, the characteristics suggested by V. G. Bogorov (1941) are not applicable to the temperate latitudes as a whole.

In the opinion of A. K. Geinrich, as we attempt to differentiate the biologic seasons in the marine plankton, we must base our discussion on different characteristics from those used by V. G. Bogorov. The annual cycle can be divided into natural segments, each of which is characterized by a definite group of seasonal species present in the plankton only during this time segment, and a definite stage in the life cycle (annual maximum) of year-round species. However, due to the gradual nature of replacement of one group of species by another, any seasonal boundaries we select are arbitrary to some extent. The clearest boundary between seasons in the cold-temperate regions is the boundary between winter and spring, which marks the beginning of the vegetation of the phytoplankton.

In the zooplankton of the cold-temperate regions of the northern hemisphere, a very important role is played by a few common genera of phytophagous copepods; *Calanus*, *Pseudocalanus*, *Metridia*, etc. Among the holoplanktonic phytophagous forms, three types of life cycles can be distinguished (Heinrich, 1961a). The first type includes species in which breeding of the first generation is related to the spring development of phytoplankton and cannot begin any earlier. This type of life cycle is exhibited by *Calanus finmarchicus*, dominant in planktonic communities of the temperate waters of the North Atlantic (Marshall, Orr, 1955; Bogorov, 1941), as a result of which the annual maximum zooplankton biomass follows the spring pulse of phytoplankton. A modification of this type is the life cycle in which breeding and growth can occur only when phytoplankton is sufficiently abundant, the transition from the last copepodite stage to the adult occurring at the beginning of the period of phytoplankton vegetation. In regions of domination of these species (e.g., *Eucalanus bungii* in the Bering Sea and northwestern Pacific), the annual maximum of zooplankton biomass is seen in the spring (Heinrich, 1957, 1961a).

The second type of life cycle is exhibited by forms, the breeding of which is independent of the quantity of phytoplankton and may occur either in spring, or in other seasons: *Calanus cristatus* and *C. plumchrus* in the North Pacific, *Metridia longa* and *C. hyperboreus* in the North Atlantic. Species with life cycles of the first and second types usually have 1-3 generations per year in the cold-temperate regions.

The third type of life cycle is that of species which can multiply throughout the year, but do so most rapidly during the period of vegetation of the phytoplankton. Most of the smaller forms of copepods fall into this group, and have several generations per year.

A. K. Heinrich (1961a) also reports that the presence in the plankton of the cold-temperate regions of certain neritic species of Cladocera and Copepoda is always a characteristic of the summer and early fall.

The breeding of predaceous copepods, for example, *Pareuchaeta* spp., in the opinion of A. K. Heinrich, is independent of the phytoplankton and is not limited by the presence of animal food, which is always sufficient; these species breed throughout the year. However, the abundance of phytoplankton does determine the success of the breeding of phytophagous zooplankton and, therefore, the food base available for the predators. Data on common pelagic polychaetes, the pteropod mollusk *Clione limacina* and chaetognaths (Kaufman, 1967; Mileikovsky, 1962, 1969, 1970; Dunbar, 1962) indicate that seasonal breeding is a common phenomenon among predatory holoplankters of the cold-temperate communities.

Among the widespread, common species, the peculiarities of the life cycle change with latitude and may differ in the southern and northern portions of their ranges. The number of generations during one reproductive season, in particular, differs with latitude: The further north, the fewer the number of generations.

In the cold-temperate zone, the nature of the sequence in maxima of biomass of phytoplankton and zooplankton is determined by the type of life cycle of the dominant species. A bicyclic annual course of development of plankton is characteristic for the entire zone; the specifics of development of plankton is characteristic for the entire zone; the specifics of development of phytoplankton and zooplankton in the waters of the North Atlantic and North Pacific differ somewhat. In the North Atlantic, with domination of *Calanus finmarchicus*, the annual maximum of zooplankton biomass follows the spring annual maximum of phytoplankton with some delay, while the autumn, smaller, maximum of phytoplankton is followed by a small autumn rise in the biomass of zooplankton. Significant consumption of phytoplankton by zooplankton begins a few weeks after the beginning of development of the phytoplankton and coincides with the appearance of the II and III copepodites--soon after the massive spawn of *C. finmarchicus* having survived the winter (Cushing, 1975). It is characteristic of the temperate waters of the North Atlantic on the whole that the spring peak of development of phytoplankton is greater than the fall peak, and that the amplitude of the fall peak varies from year to year.

In the northwest Pacific and the Bering Sea, where the common species in zooplankton are *C. cristatus*, *C. pacificus*, *C. plumchrus* and *Eucalanus bungii* (the first three species are Pacific analogs of the North Atlantic), the bicyclic development of phytoplankton, "normal" for temperate waters, is observed only in the neritic regions. In the oceanic regions, only a fall maximum of biomass of phytoplankton is observed, while the annual maximum of zooplankton biomass occurs in the spring and summer, when the phytoplankton is rather abundant (Heinrich, 1961a).

The duration of the production cycle of plankton varies from one month to one year, averaging three months for phytoplankton and six to seven months for zooplankton. The fluctuations in production cycles of plankton from year to year reach two or three orders of magnitude as to population of algae and one or two orders for the biomass of animals. The differences between the mean values for different years in the same regions are less than between different seasons in the same year (Cushing, 1975).

The mean value of annual production of planktonic phytophages in productive regions, where they represent most of the biomass in the 0-500 m layer, has been estimated as 200-300 mg/m^3 (Greze, 1973a).

We must note one important specific feature of the cold-temperate regions of the northern hemisphere which is becoming more significant with each passing year: the continuous increase in the effects of anthropogenic factors on the plankton communities, particularly water pollution. These waters wash the shores of the most industrially developed countries in the world, and their coast sections are the most polluted portions of the world ocean. Pollution has a significant and ever increasing effect on the biology of plankton communities in most regions in this zone. To illustrate this statement, it is sufficient to present two examples. In the northwestern Atlantic, over the edge of the continental shelf and somewhat further out to sea, lumps of tar floating on the surface now equal more than 20% of the wet weight of all neuston (Morris, 1971). Between Hawaii and Japan for mile after mile, one observes films of copepod remains, which have died as a result of pollution of the water along the coast of Japan (Lee, Williams, 1974).

3.2 Planktonic Communities of the Boreal Atlantic

The pelagic communities of the Boreal waters of the North Atlantic are related in their distribution to the superficial subarctic water mass (Mamayev, 1960; Jaschnov, 1961; Grainger, 1964; C. W. Beklemishev, 1969). Within this area, a number of large regions can be distinguished, differing in their latitudinal position, the presence of a more or less closed system of water circulation and, as a result, the structure of the planktonic communities and the dynamics of seasonal processes. These relatively independent regions include the Norwegian Sea with its circulation formed by the system of Norwegian and East Iceland Currents; the Labrador Basin, with the circulation of the West Greenland and Labrador Currents; the open portion of the North Atlantic, to the north of the main flow of the North Atlantic Current, with its less clear circulation formed by the peripheral streams of the North Atlantic Current, the Irminger Current, and the eastern branch of the Labrador Current.* One general regularity in the hydrologic mode of these regions is the predominance of cyclonic water circulation. Cyclonic flow also predominates in the movement of air masses here (Bulatov, 1971). This creates favorable conditions for upwelling of deep water, rich in biogenic elements, and, therefore, for abundant development of plankton and the formation of concentrations of commercial fish.

The taxonomic composition of the zooplankton of the Norwegian Sea, the Labrador Basin and adjacent waters in the open North Atlantic is similar in its main features, the difference resulting from the intrusion of warm-water elements with the waters of the North Atlantic Current and cold-water forms with the Arctic waters.

The predominant role is that of the copepods, particularly the most abundant species, _Calanus finmarchicus_ s.l. During some seasons in the Norwegian Sea and the Labrador Basin, these crustaceans may represent more than 90% of the biomass of all zooplankton. The growth and development of _C. finmarchicus_ from egg to the older copepodite stages produces the summer increase in total biomass and the maximum concentrations of plankton. The population of _C. finmarchicus_ in the 0-200 m layer decreases in the fall, as a result of intensive predation by planktophagous fish, and also due to the gradual descent of the fourth and fifth copepodite stages into the depths, where they spend the winter.

Due to the existence of more or less closed systems of water circulation, the Labrador Basin and Norwegian Sea support large, independent populations of _C. finmarchicus_ s.l. It is more difficult to determine the nature of the population of the species inhabiting the open waters of the North Atlantic. Doubtless, it is supplemented by constant intrusion of a portion

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*In accordance with the purpose of the present monograph, primary attention will be given to oceanic plankton communities, while the regions of the North Sea, the Grand Banks and the Gulf of Maine will not be analyzed.

of the population from the Labrador Basin, which communicates broadly with the adjacent waters of the open North Atlantic. The North Atlantic Current may carry these crustaceans to the northeast and even through the Faeroe-Shetland Channel into the southern area of the Norwegian Sea. On the other hand, a portion of the population of *C. finmarchicus* from the Norwegian Sea is carried along with the East Iceland Current into the open North Atlantic and subsequently may be carried to the south and west. Thus, these two, large, independent populations of this species may be interconnected by means of a third population, less numerous and more or less dependent on the first two. We should keep in mind the fact that, in spite of the predominance of transport water in the northeastern direction, the open portion of the North Atlantic which we are considering does have its own cyclonic system of circulation of water masses, though it is highly complex and not clearly expressed. Therefore, the population of *C. finmarchicus* which inhabits this area cannot be considered totally dependent. In part, it may be drawn into the circulation or may be delayed for an indefinite period in any portion of the circulation due to eddies in the current, e.g., in the region of the Irminger Sea.

In zones of mixing of subarctic waters with the waters of the Polar Basin (Davis Strait, northeast of the Norwegian Sea), *C. finmarchicus* s. str. is found together with its close relative *C. glacialis* and with *C. hyperboreus*--species which occupy the Arctic area, but penetrate with streams of cold water into the temperate latitudes (Jaschnov, 1963, 1970). To the south of the Faeroe-Shetland Channel, in the northeastern Atlantic, *C. finmarchicus* s. str. is found together with another relative species--*C. helgolandicus* (Marshall, Orr, 1955; Jaschnov, 1961). This species, a part of the Lusitanian faunistic complex, is carried into the Norwegian Sea and the nrothwest Atlantic only sporadically. In contrast to the species we have mentioned, *C. finmarchicus* s. str. is a true boreal species, endemic for the temperate regions of the Atlantic Ocean (Jaschnov, 1961, 1970).

Among other species of copepod filter feeders, in the boreal waters of the North Atlantic, *Pseudocalanus elongatus* and *P. minutus* are present in great quantities. The former (smaller) species is particularly numerous in shallow waters over the shelf; the latter is found primarily in the oceanic zone and plays a significant role in the pelagic communities of the Labrador Basin (Pavshtiks, 1969; Kielhorn, 1952) and the Norwegian Sea (Pavshtiks, Timokhina, 1972; Wiborg, 1954). These species are morphologically difficult to distinguish, and their biology has not been sufficiently studied. Their reproductive season is quite extended: practically all summer, in addition to the mature individuals of both species, the plankton contains their nauplial and early copepodite stages. Obviously, during the year *P. elongatus* and *P. minutus* breed several times, but different breeding periods are difficult to distinguish. The greatest number of *Pseudocalanus* in different years in the North Atlantic may occur in different months during the spring, summer or fall; in the Norwegian Sea it is most frequently observed in the summer or fall (Gruzov, 1963; Wiborg, 1954, 1955). In contrast to the Norwegian and Labrador Seas, in the open North Atlantic, *Pseudocalanus* spp. are not a significant fraction of the plankton, being usually replaced by more thermophilic and oceanic species of the genera *Paracalanus*, *Ctenocalanus* and *Clausocalanus*, which, in spite of their small size, sometimes represent a significant fraction of the zooplankton biomass (Kanaeva, 1962). In the Labrador Basin and the Norwegian Sea, *Paracalanus* and *Clausocalanus* are not numerous.

Yet another small species of copepod reaches significant numbers in the boreal waters of the North Atlantic--*Microcalanus pusillus*. Information on its life cycle and the nature of its feeding is almost totally absent from the literature. It is assumed (S. M. Marshall, 1949) that *M. pusillus* feeds on flagellatae.

Among the copepods with mixed diet, *Metridia lucens* is most important in the North Atlantic, being ubiquitous, although it is most frequently encountered in the southern portion of the boreal area: in the region of the Flemish Cape Bank, in the open waters of the boreal Atlantic, in the southern part of the Norwegian Sea (Kanaeva, 1963; Semenova, 1964; Timokhina, 1968). However, this species never represents a great biomass and, in this respect, is quite different from the similar Far Eastern species *M. pacifica*, which may form significant concentrations. The breeding season of *M. lucens* in the North Atlantic is extended: The nauplii and juvenile forms are encountered throughout the year, though most numerous in spring and fall; the species achieves its highest number in late summer (Gruzov, 1963). Another species of the genus--*M. longa*--is an Arctic one, although it can penetrate far into the temperate regions with cold currents, where it usually is seen together with *C. glacialis* and *C. hyperboreus*. In mixed waters in the northern part of the boreal area, *M. longa* is quite common and, due to its large dimensions, may represent a significant fraction of the zooplankton biomass (Pavshtiks, 1964; Timokhina, 1968). In the open waters of the boreal Atlantic, in the southern portion of the Labrador and Norwegian Seas, *Pleuromamma robusta* is rather common, and sometimes one also sees *P. abdominalis*, *P. xiphias*, *P. borealis* and *P. gracilis*, which are common in the subtropics and reach the southern portion of the boreal area with the North Atlantic Current.

Among the other euryphagous copepods for the boreal Atlantic, we should note *Scolecithricella minor*. The small euryphagous calanoids form a unique complex: *Acartia clausi*, *Centropages hamatus*, *C. typicus*, *Temora longicornis*. They are found primarily in the neritic zone, but extend widely into the central waters of the Labrador Basin and the Norwegian Sea as well. Their numbers may be relatively high, particularly in late summer-early fall, but due to their small size they usually are not significant in the total mass of plankton. Their breeding period is extended, occurring primarily in the spring and summer. They are rare in the open waters of the North Atlantic.

There are not many abundant species of predaceous copepods in the boreal area of the Atlantic. The most important one is *Pareuchaeta norvegica*, which, due to its large size and ability to form concentrations, plays a significant role in the pelagic community and represents an important component in the nutrition of the planktophagous fish. Furthermore, *P. norvegica*, extending over a broad range of depths, is frequently eaten by commercial fish, such as young redfish (Konchina, 1968). The same is true of *Heterorhabdus norvegicus*, although this copepod is not numerous and its role in the plankton is much more modest. Not being related to the period of vegetation of the phytoplankton, the predaceous copepods breed year-round and may be greatest in number when the phytophages are at their period of minimal development, for example, during the fall and winter season, as is observed for *P. norvegica* in the Norwegian Sea.

The Cyclopoida are represented in the plankton of the boreal Atlantic primarily by species of the families Oithonidae and Oncaeidae, which include some abundant species: the cosmopolitan *Oithona similis*, the Arctic-boreal *Oncaea borealis* and the boreal *Oithona atlantica* and *Oncaea conifera*. The population of *O. similis* is relatively large throughout the year, forming a sort of background against which the peaks of development of the other plentiful species of copepods appear in sequence. In winter, when the number of other copepods decreases, *O. similis* moves to first place, composing 60-70% of the total number of zooplankton. In contrast to it, *O. borealis* has its peak in number in late spring and early summer. During this period in the Norwegian Sea it may amount to 10-30% of the total zooplankton population; this is significant, recalling that in this season the total number of planktonic animals is generally quite high (Gruzov, 1963). Approximately the same relationships are characteristic for these species in the Labrador Basin (Pavshtiks, 1966). In the open waters of the boreal Atlantic, the significance of *O. atlantica* and *O. conifera*, which are not numerous in the northern portion of the boreal area, increases.

The next group after the copepods, quite important in the creation of high biomasses of zooplankton in the boreal Atlantic, is the Euphausiacea. Of these, most numerous are *Thysanoessa longicaudata* and *Meganyctiphanes norvegica*--boreal oceanic species. *Th. longicaudata* forms accumulations primarily in the surface zone. *M. norvegica* is less numerous and is encountered primarily at depths of 200-500 m, though it frequently rises to the surface. Both species are euryphagous, feeding primarily on detritus and phytoplankton (Mauchline, Fisher, 1969); therefore, their life cycle is related to the period of vegetation of the planktonic algae. The reproductive season of *Th. longicaudata* in the Labrador Basin extends from May through September, with the greatest number observed in July-August, while in winter only mature individuals are seen (Kielhorn, 1952). In waters of Atlantic origin in the Norwegian Sea, the greatest biomass of euphausiids is seen in May and June (Gruzov, 1963; Timokhina, 1968).

Among the boreal hyperiid amphipods, *Parathemisto abyssorum* is most important in the North Atlantic. Juvenile *Parathemisto* are seen in the largest numbers in spring and early summer.

The groups of planktonic crustaceans which we have considered: copepods, euphausiids and hyperiids, are determinant in the formation of the food supply for commercial planktophagous fish. In addition to them, the active planktonic predators are quite significant in the Atlantic boreal communities:

the Chaetognatha, Hydromedusae and Ctenophora. Though they do not make a significant fraction of the diet of the animals at higher trophic levels they, nevertheless, may influence their distribution, by consuming the planktonic crustaceans to a significant extent and greatly reducing their biomass. Of the chaetognaths, the most numerous are *Sagitta elegans* and *Eukrohnia hamata*, regularly encountered in the plankton throughout the year. Their greatest numbers are observed in the Norwegian Sea in late spring and early summer (Gruzov, 1963), when they may represent up to 20% of the plankton biomass. In the Labrador Basin, they are also present in the plankton throughout the year: *S. elegans* is encountered primarily in the surface zone near the continental slope, while *E. hamata* is more oceanically distributed and is found over a greater range of depths (Kielhorn, 1952). The chaetognaths are not as important in the boreal communities of the Atlantic as they are in certain tropical communities of the world ocean, either in terms of number or in terms of biomass.

The hydromedusa *Aglantha digitale*, widespread in the Arctic and temperate regions, may form great concentrations in the temperate waters of the North Atlantic. In the central regions of the Norwegian Sea, it develops in large numbers, regardless of the hydrologic conditions of the year, approximately one month after *C. finmarchicus* s.l. reaches its maximum population, usually in July. At this point there is a sudden drop in the population and biomass of *Calanus* (Timokhina, 1968). A negative correlation has been found between the population of *A. digitale* and *C. finmarchicus* s.l. (Gruzov, 1963; Pavshtiks, 1964).

Seasonal changes in the plankton communities of the boreal Atlantic have been studied in some detail for the Norwegian Sea, less for the Labrador Basin, and still less for the open waters of the boreal Atlantic. The season of biologic spring, characterized by the maximum development of phytoplankton and the beginning of breeding of *C. finmarchicus* s.l., the Euphausiacea and certain others, begins earliest in the southern regions of the boreal area, then gradually extends northward, being delayed in the northern boreal waters by 2-3 months in comparison to the southern boreal waters. Figure 10, based on the data of Pavshtiks (1966, 1969), Timokhina (1962), Semenova (1964), Colebrook and Robinson (1965), shows the times when biologic spring begins in the various regions of the boreal Atlantic. Spring starts in the coastal waters of the southern boreal zone (February-March), then encompasses the regions of the North Sea and the oceanic area of the Atlantic south of 59°N (March-April). In May and June, biologic spring extends to the central regions of the Labrador Basin and the Norwegian Sea and, finally, in June-July, biologic spring extends into the northern boreal regions of the Davis Strait and the northeastern area of the Norwegian Sea. The maximum development of phytoplankton is followed by a gradual increase in the biomass of phytophages. In the southern boreal regions, the times of the maxima are closer together (Fig. 11). In the Central areas of the Norwegian and Labrador Seas, the maximum biomass of zooplankton is delayed by approximately one month relative to the peak of production of phytoplankton: In the central waters of the Norwegian Sea, the maximum biomass of *Calanus* usually occurs in June.

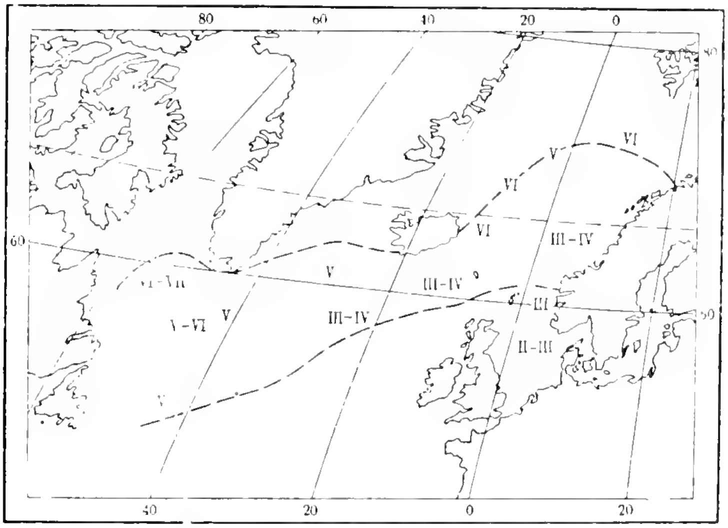
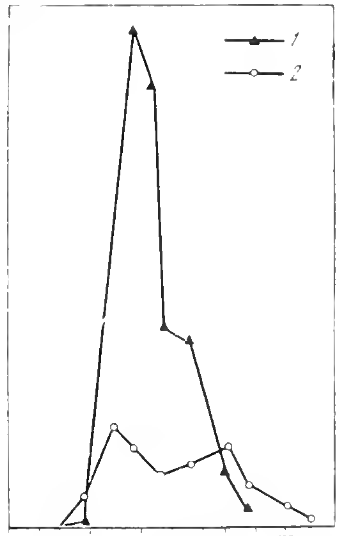


Fig. 10. Times (months) of onset of biologic spring in various regions of the boreal Atlantic (Pavshtiks, 1968; Pavshtiks, Timokhina, 1972; Colebrook, Robinson, 1965).

Fig. 11. Times of maximum development of phytoplankton and of the biomass of copepods in the southern boreal waters of the open Atlantic (Colebrook, Robinson, 1965). 1, Phytoplankton number; 2, Copepod number (relative values).



During the year, the maxima of population of the individual species follow one another in sequence. This phenomenon has been analyzed in detail by L. N. Gruzov (1963) for various regions of the Norwegian Sea. The relative significance of individual species in the community also changes significantly from season to season. The differences from year to year in the development of plankton have been most thoroughly studied for the Norwegian Sea. Although in the open regions of the North Atlantic, regular multiannual collections of plankton have also been made using an automatic continuous plankton recorder, these data are difficult to compare with the materials obtained using plankton nets. The differences from year to year in the development of the plankton of the Labrador Basin have not been studied, but it has been demonstrated for the Norwegian Sea (Pavshtiks, Timokhina, 1972) that the beginning of biologic spring and the duration of the seasons in the plankton depend on many abiotic factors, particularly the number of sunny, storm-free days in March and April, the intensity of the influx of warm water with the Norwegian Current, the degree of summer heating of the water, etc. Storms and overall cloud cover during the spring months delay the development of phytoplankton and the subsequent mass breeding of the crustaceans. During relatively cold years (1958, 1962, 1965, 1966), a delay and an extension in the time of biologic spring has been observed in comparison to moderately warm or warm (1960) years. Depending on abiotic factors, the interrelationships of species within a community change from year to year. For example, the largest number of the hydromedusa *A. digitale* occurs during cold years (1962-1963), the maximum biomass--during warm years (1960-1961) (Timokhina, 1968). Apparently, this is a result of the more rapid growth of medusae during warm years. Since the number of medusae influences the number of planktonic crustaceans, during different years the production of different links in the plankton community may differ significantly (Table 4).

Table 4. Production of main forms of zooplankton over entire Norwegian Sea area, occupied by Atlantic waters, in 1959-1963 (in millions of tons) (Timokhina, 1968).

Species	1959	1960	1961	1962	1963
Calanus finmarchicus	7.33	6.46	4.13	8.51	4.88
Calanus hyperboreus	2.24	0.58	1.01	3.07	0.24
Metridia longa	1.64	1.00	0.57	2.59	0.94
Metridia lucens	0.36	0.007	0.20	--	0.44
Pseudocalanus elongatus	0.64	0.39	0.21	0.26	0.44
Oithona similis	0.35	0.007	0.007	0.17	0.17
Oithona atlantica	0.16	0.03	0.05	0.25	0.32
Oncaea borealis	0.13	--	0.007	0.15	0.29
Aglantha digitale	8.40	20.89	21.51	49.90	20.10
Chaetognatha	6.40	3.69	1.08	1.84	0.84

According to the classification of V. G. Bogorov (1967), the boreal area of the North Atlantic must be considered a highly productive region of the world ocean. During the spring and summer, the biomass of zooplankton in many regions of the Labrador Basin and the Norwegian Sea reaches 500 mg/m^3, in many cases exceeding 1000 mg/m^3 (Pavshtiks, 1966; Timokhina, 1968; Vladimirskaya, 1972). The biomass of all seston may be 2-3 times greater. In the fall and winter season, the biomass is relatively low, rarely exceeding 50 mg/m^3.

An attempt to calculate the production of main components of plankton communities in various water masses of the Norwegian Sea was made by A. F. Timokhina (1968). Based on the materials of multiannual seasonal plankton surveys, the annual production of the most numerous representatives of the zooplankton in the Atlantic and mixed waters of the Norwegian Sea has been calculated, and is presented in Table 5. These quantities should be considered as minimal, since they do not include the production of the euphausiids or hyperiids, due to the insufficient degree of study of the annual dynamics of the number of these groups; the production of medusae, on the other hand, may be exaggerated, since the calculations were based on wet weight. The maximum annual production of phytophagous zooplankton in the Atlantic waters of the Norwegian Sea is 22 g/m^2, in the mixed waters--73 g/m^2 wet weight, corresponding to 1.64 and 5.51 g C, or 19 and 67 kcal beneath each square meter. These values are more than an order of magnitude lower than the values of primary production calculated for these regions: 70-200 g C/m^2, i.e., 650-2000 kcal/m^2 (Vinberg, 1960). Thus, in the Atlantic waters of the Norwegian Sea, phytoplankton is to some extent underutilized by the phytophagous zooplankton.

Table 5. Production of mass planktonic species beneath entire area of Norwegian Sea occupied by mixed and Atlantic waters, average for 1959-1963 (millions of tons) (Timokhina, 1968).

Species	Mixed waters	Atlantic waters	Maximum annual production
Calanus finmarchicus	5.58	6.26	16.96
Calanus hyperboreus	0.74	1.42	3.07
Metridia longa	1.41	1.34	2.59
Metridia lucens	0.01	0.20	0.44
Pseudocalanus elongatus	0.86	0.38	1.99
Oithona similis	0.05	0.14	0.35
Oithona atlantica	0.07	0.16	0.32
Oncaea borealis	0.08	0.11	0.29
Aglantha digitale	6.11	24.16	49.90
Chaetognatha	0.92	2.77	6.40
Total	15.83	36.94	--

Keeping in mind the similarity of the quantitative development of plankton in the Norwegian Sea and the Labrador Basin, and also considering the great extent of the areas of open water in the boreal Atlantic, it is apparently not a great exaggeration to assume that for the entire boreal Atlantic area the production of the zooplankton community is 2 to 2.5 times greater than the production calculated for the area of the Norwegian Sea.

3.3 Planktonic Communities of the Boreal Pacific

In our analysis of the biology of the North Pacific, it is proper to include in the water area under consideration the actual oceanic waters and the Far Eastern seas: the Bering Sea, Sea of Okhotsk and Japan Sea. The unique features of each of these seas, resulting from differences in their hydrologic modes, latitudinal position and other factors, cause differences in the makeup of their planktonic populations as well. Also, the boundary between two biogeographic areas, the northern Pacific temperate and circumtropical areas, passes through the Japan Sea (Brodsky, 1957; Zenkevich, 1963). This makes it desirable to analyze the planktonic communities for each of these seas individually.

Sea of Okhotsk. The planktonic communities of the Sea of Okhotsk include cold-water and cold-temperate species, and at the very southern region of the sea adds the oceanic species typical for the warm waters of the northwestern Pacific. It is most efficient to distinguish three communities in the plankton of the sea: the oceanic subarctic, oceanic cold temperate and neritic communities.

The oceanic subarctic community occupies the entire northern portion of the sea, except for the coastal zone, and extends southward to 56°N, where it is replaced by the next community. Along the shores of Sakhalin, this community extends to the latitude of Cape Patience (Mys Terpenia). The primary components of the zooplankton of this community are: *Calanus glacialis*, *Metridia ochotensis*, *Parathemisto libellula* and *Thysanoessa raschii*. At the end of the summer, the biomass of *C. glacialis* in the 0-100 m layer in some locations reaches 8000 mg/m^3, making up as much as 90% of the entire biomass of zooplankton. In the northernmost region of the sea, *C. glacialis* is found everywhere, but is less numerous. It extends to the south along the shore of Sakhalin together with the cold current, but plunges to a depth of over 200 m, so that its quantity in the upper productive layer is not great (Ponomareva, 1961).

Metridia ochotensis is widespread, forms concentrations and is important in the diet of the Okhotsk herring (up to 45-50% of the diet). The main concentrations of this crustacean are observed in the northern and western portions of the sea, the biomass sometimes reaching 1000-5000 mg/m^3 in the 0-100 m layer. In the summer and autumn, when the surface temperature of the water in the southern portion of the sea reaches 15 C, *M. ochotensis* is encountered individually, but in the spring the number becomes quite high (in the southernmost portion of the sea, up to 5000 mg/m^3 in the 0-100 m layer).

Parathemisto libellula is common in the waters of the Arctic structure. This species is eagerly eaten by planktophagous fish, particularly herring. In the northern regions of the sea, *P. libellula* makes up to 90% of the diet of the herring. Concentrations of *P. libellula* with a biomass of up to 250 mg/m^3 have been reported in the northeastern and Shantar Is. regions. In the central and eastern regions of the sea, *P. libellula* does not extend further south than 56°N, along the eastern shores of Sakhalin it reaches as far south as 53°N, gradually submerging from the surface layer to the 100-200 m layer.

Thysanoessa rashii dominates among the euphausiids. In the fall, it is encountered in the greatest quantities (up to 2500 mg/m^3) along the shores of Sakhalin and Kamchatka, particularly in the northwestern portion of the sea (Ponomareva, 1959). In addition to these numerous species, the oceanic cold-water community includes the copepods *Derjuginia tolli* and comb-jelly *Mertensia ovum*.

The main components of the oceanic cold-temperate community are *Calanus plumchrus*, *C. cristatus*, *Eucalanus bungii*, *Metridia pacifica*, *Parathemisto japonica*, *Thysanoessa inermis*, and *Th. longipes*. *C. plumchrus* is quite widespread and forms large concentrations in the surface 100 meter layer. It, together with the euphausiids, is the basis of the diet of the planktophagous fish. The maximum biomass of *C. plumchrus* in the summer and fall is found in the central region--up to 600-2000 mg/m^3 (1959), though it inhabits the northeastern portion of the sea in large quantities as well. North of 57°N, the population of *C. plumchrus* plummets rapidly. *C. cristatus* is encountered in largest quantities in the southern portion of the sea, along the Kurile Islands, where its biomass in the 0-100 m layer may reach 500-700 mg/m^3; in the central portion of the sea, it is not numerous. *Eucalanus bungii* is also scarce, its biomass reaching 200 mg/m^3 (in the 0-100 m layer) only in the southern portion of the sea.

Metridia pacifica extends throughout almost the entire sea, except for its southwestern portion. The biomass is almost always less than 10 mg/m^3, but sometimes reaches 200 mg/m^3. The northern boundary of large numbers of this species, like that of *C. plumchrus*, is at approximately 57°N.

Thysanoessa longipes and *T. inermis* basically determine the biomass of the euphausiids in the Sea of Okhotsk. The former species is encountered in significant numbers along the coast of Kamchatka, and in the south of the sea its maximum biomass--up to 3000 mg/m^3--is observed in the spring in the southern portion, in the summer and fall north of 55°N. *T. longipes* does not form large concentrations, but is encountered almost throughout the entire oceanic zone of the sea. The biomass of this species reaches 500-1000 mg/m^3 (Ponomareva, 1963).

The warm-water oceanic community in the Sea of Okhotsk is found only in the zone of influence of the Soya Current, i.e., in the extreme south of the sea, in La Perouse, Ecatherine and Vries Straits (Brodsky, 1955). Characteristic species of the community are: *Labidocera japonica*, *L. bipinnata*, *Candacia bipinnata*, species of *Euchaeta* and *Corycaeus*, *Evadne tergestina*, and salps.

This same community includes Euphausia pacifica, encountered in the Sea of Okhotsk primarily near the Kurile Islands (up to 1000 mg/m^3), and in the central portion of the sea only in very small numbers during the period of greatest warming of the surface waters; apparently, it does not breed in this area.

The zone occupied by the neritic community is located along the shores of the sea in a narrow strip extending along the northern shallow water zones. This community includes larvae of benthic invertebrates and neritic holozooplankton, consisting primarily of cold-water species.

Japan Sea. The Japan Sea is distinguished by the diverse composition and great variety of its plankton communities.

Among the copepods, Pseudocalanus elongatus, and particularly Calanus glacialis, are very important, encountered in the greatest numbers in the southern portion of the Tatar Strait, extending to the south along the continent with the cold Primorye Current as far as the shores of Korea (Meshcheryakova, 1960).

The community of the southwestern Sakhalin waters includes a number of subtropical, in summer even tropical species and, at the same time, some northern species (Ponomareva, 1954). A few individuals of the Okhotsk Metridia ochotensis reach this area through La Perouse Strait.

In the western portion of the sea, the communities of Possiet and Amur Bays are characteristic (Brodsky, 1957). In Possiet Bay, representatives of subtropical and even tropical fauna are encountered; this warm-water community populates the waters of the coast of Korea, along the eastern shore of which a branch of a warm current flows (Uda, 1934). The community of Amur Bay differs from the Possiet community in that it includes no tropical species.

In the open portion of the sea, there are two communities: the northern and southern communities, with their boundary at approximately 40°N. Of course, the position of this boundary varies from season to season and from year to year, depending on the pulsations of the currents. The 40th parallel is the boundary between the boreal and subtropical planktonic fauna.

The plankton of the Japan Sea is quantitatively rich, the biomass of plankton in the open portion of the sea reaching 800 mg/m^3, along the coast as high as 2000 mg/m^3. The biomass consists of calanids (C. plumchrus, C. pacificus, and in the north C. glacialis as well) and euphausiids (Th. inermis, Th. longipes, and in the north also Th. raschii, in the south--Euphausia pacifica). In some areas, Parathemisto japonica plays an important role in the biomass of the plankton.

Northern portion of the Pacific Ocean and Bering Sea. In the Bering Sea, five distinct plankton communities can be differentiated (Brodsky, 1955; Vinogradov, 1956). The southern oceanic community is quite similar in its specific composition to the oceanic community of the extreme northern portion of the Pacific Ocean, which is natural, considering the hydrologic similarity of the two areas. The most important characteristic species are *Calanus cristatus*, *C. plumchrus* are replaced by *C. glacialis* and *Th. raschii*. Certain cold-water species of the latter community descend with the Anadyr Current to the south to Kamchatka and, together with the neritic species, make up the western Bering-Sea neritic community, similar in its specific composition to the eastern neritic community of this sea. In Anadyr Bay and along the shores of Alaska, there is a neritic community, characteristic of slightly less saline water. The primary species are *Centropages memurrichi*, *Acartia clausi*, *A. longiremis* and, particularly, *Podon leukarti* (up to 600 indiv./m^3 in the surface waters).

At depths of over 200 m in the southern portion of the sea there is a deep-water Bering Sea community--derivation of the boreal Pacific Ocean deep-water community.

The main abundant species of plankton in the Northern Pacific Ocean (*C. plumchrus*, *E. bungii*, *Parathemisto japonica*, *Euphausia pacifica*, *Metridia pacifica* beneath the thermocline and *C. cristatus* above it) form concentrations with a very high biomass--up to 2000 mg/m^3.

After the spring rise of *E. bungii*, *C. plumchrus*, *C. cristatus*, *Thysanoessa raschii* and *T. inermis* to the surface, their biomass in the 0-100 m layer is up to 2500 mg/m^3.

The boreal waters of the northern Pacific as a whole are characterized by a plankton biomass in the upper 100 meter layer on the order of 200-1000 mg/m^3. In the south, these waters meet the warm waters of Kuroshio, in which the biomass of plankton is 10-20 times less (Bogorov, Vinogradov, 1955).

The Kuroshio waters contain a completely different plankton community, including a significant quantity of tropical species. In the mixing area between these waters and the boreal waters of the North Pacific, there is an ecotone community, including both boreal and tropical areas in the plankton.

4. Communities of the Temperate and Cold Waters of the Southern Hemisphere.

(N. M. Voronina)

The population of the pelagic zone of the temperate and polar latitudes inhabit biotopes with characteristically sudden changes in environment during the course of the year (see Chapter I.2 II.2). As we know, the essence of the seasonal differences in the pelagic realm is related to changes in solar radiation which, on the one hand, determine the quantity of light penetrating the water, and on the other hand, the processes of heat exchange, causing heating and cooling of the surface waters, formation and thawing of ice and, as a result, changes in the thermal and density stratification. These changes, in turn, influence the delivery of nutrient salts to the euphotic layer.

Let us take a look at how these factors are reflected in the structure and functioning of the pelagic communities of the Antarctic and Subantarctic.

4.1 Phytocenes

Factors defining the quantitative development of phytoplankton. In Antarctic waters, the concentration of phosphates and nitrates, even during the phytoplankton bloom and the period of maximum stability of the surface layer, when their upward travel is hindered, remain higher than in the winter in the temperate waters of the northern hemisphere. Therefore, they cannot be considered as limiting factors (Hart, 1934; Bogoyavlenskiy, 1958; El-Sayed, 1968b). The reason for the exceptional richness of this area in nutrient salts is the constant renewal of their reserves resulting from the general character of circulation of the deep water with predominance of upwelling. Only the decrease in the quantity of silicates, the maximum concentrations of which are located deeper than the other biogens, may play a partial role in the post-maximal decrease in the population of diatoms (Clowes, 1938; Hart, 1934; Arzhanova, 1974).

The Subantarctic is significantly poorer in nutrients; a decrease in their quantity is observed as we move northward. However, even in the Subantarctic, the concentration of phosphates does not drop to a level low enough to limit the rate of cell division of algae in experiments (Kuenzler, Ketchum, 1962; Lewin, Guilland, 1963). The addition of a mixture of nutrient salts to Antarctic and Subantarctic water in experiments did not cause an increase in primary production (Kabanova et al., 1974a). It can be said with certainty that in the Southern Ocean, the concentration of nutrients does not limit development of phytoplankton. The inverse correlation between the abundance of phytoplankton and the concentration of phosphates established by Hardy and Gunter (1935) confirms this opinion quite clearly.

Light is of dominating significance for the vital activity of algae. In the higher latitudes, the total solar radiation during the course of the year fluctuates widely. The time of onset of the light season and its duration differ at different latitudes. The period with minimum solar radiation (below 10 kcal/cm^2/month) extends at 60°S from February through the end of November, at 40°S--only from March to early October, two and one half months shorter.

As the illumination increases, the rate of photosynthesis increases up to a certain limit--to the point of light saturation. This point is not the same at different latitudes (Steemann Nielsen, 1963) or for different groups of algae (Ryther, 1956). Strickland (1958) reached the conclusion that the maximum growth of mixed populations of algae occurs with an intensity of incident radiation of over 0.15 cal/cm^2/min, while severe suppression of growth occurs at over 0.5 cal/cm^2/min. Using data on the mean monthly radiation (Braginskaya et al., 1966) and the duration of the light time (Dubovskiy, 1966) to calculate the mean daily radiation, then comparing it with the conclusions of Strickland, we can see that the light factor limits the development of algae at the surface at 60°S from May through August, at 70°C--from April through July. However, in the extreme south, some areas are freed of ice rather late (Fig. 12), when the illumination is beginning to subside, and as a result of this, the period of optimum light is briefer there.

A mean daily level of radiation sufficient to suppress photosynthesis is reached at 40°S only in December; further south--it is never reached. Thus, in the first approximation (ignoring daily changes in radiation), we can

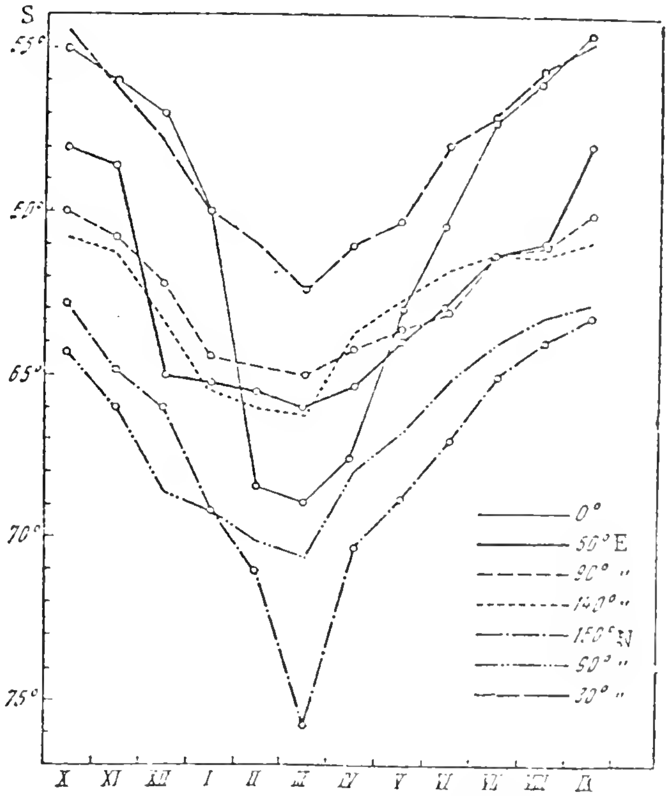


Fig. 12. Variation in position of northern limit of icepack during the course of the year at various meridians (after Eskin, 1966).

state that over most of the Southern Ocean, the suppressing effect of this factor does not appear.

The absence of light suppression of photosynthesis is obvious from numerous data on primary production vertical distribution (El-Sayed, 1968a).

The thickness of the euphotic layer is determined by the position of the compensation point. In works on primary production, it has been the practice to consider it to be located at the depth to which 1% of the incident light penetrates. In the Southern Ocean, this depth varies during the summer season from 7 to 95 m (Hasle, 1969; El-Sayed, 1968a, 1970b; Steyaert, 1973), depending on the height of the sun over the horizon and the quantity of phytoplankton present (Sverdrup, 1953; Hart, 1962). In 78% of cases, the compensation point is at a depth of less than 50 m. This means that the production upon which the population of the entire mass of the ocean feeds is formed in this very thin layer.

The beginning of the light season is a necessary, but hardly sufficient condition for the development of phytoplankton. In the spring, when the entire layer of surface water down to a depth of 100-200 m is well mixed, cells are drawn away from the surface into the unlit depths, where respiration predominates over photosynthesis. Therefore, in order for the development of phytoplankton to begin, it is very important for the summer pycnocline to form, limiting the vertical extent of the convection layer, and for stable stratification to occur, helping the cells to remain for a longer period of time at the surface.

Changes in the density structure of the water occur as a result of thawing of ice or the spring rise in temperature over the water area which is free of ice. Both of these processes lead to development of a layer of low density, the thickness of which depends on the intensity of wind mixing. Usually, it increases within the limits of the Antarctic from 10-20 m in the south to 80-100 m in the north, being 40-60 m in most regions, i.e., near the thickness of the euphotic layer. The lower boundary of the summer transformed water is characterized by an increase in the density gradient (Makerov, 1956). The vertical stability, reflecting the character of the change in density with depth, is great throughout the entire surface layer during the warm season in the high latitudes. Further north, there is a fairly thick mixed layer. The development of the mixed layer is characteristically lower and the region with high stability has a greater longitudinal spread in the Atlantic sector than in the eastern portions of the Pacific and Indian Ocean sectors. For example, at the 0° meridian, the value of $E \cdot 10^5 > 1000$ in the 0-50 m layer extends from the edge of the ice right up to 55°30'S, while at 78°W, it extends only to 66°S, and at 115°E--to 63°30'S (Ishino, 1963). This is apparently related to the significant differences in the conditions of formation of the summer stratification. Since the changes in the density structure of the water between the -2 C and the +2 C isotherms are determined almost entirely by salinity, differences in the ice content of the individual water areas become decisive in their significance (see Fig. 12). In the Atlantic sector, the maximum winter extent of the icepack reaches 54°S. while the summer ice rim lies at around 70°, but in the eastern parts of the Indian and Pacific Ocean sectors the ice does not extend as far to the north, and the seasonal movements of the boundary amount to only 4-7°. In the central portion of the Pacific Ocean sector (120-150°W), where the seasonal movements of the ice boundary amount to about 10°, high stability is observed over the entire Antarctic zone (Hasle, 1969). In general features, the boundaries of the maximum extent of the icepack in winter agree well with the areas of stability of water in the surface layer. Individual, local deviations are explained by vertical movement of the water, related to the topography of the bottom (Ishino, 1963) or frontal zones. In the more northern regions, where the summer stratification is formed only due to heating of the surface layer, its stability is significantly lower.

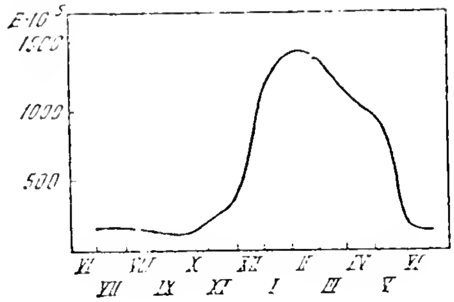
The formation of the summer type of density structure of the water begins in the northern Antarctic zone in mid-October (Fig. 13); in the Southern Antarctic later. The duration of its existence varies from 6 months in the region of the convergence to 1-2 months in the high latitudes (Makerov, 1956).

Seasonal changes in the quantity of phytoplankton. The beginning of the development of phytoplankton is determined by the increase of light intensity and the formation of density stratification. What are its subsequent changes? Long-term observations in the open waters of the Southern Ocean have never been performed, and our concept of the seasonal development of the plankton is therefore based on the results of summarization of materials from cruises. Hart (1942) divided the Antarctic water area into three latitudinal zones and averaged for each of them by months all the quantitative data on phytoplankton, based on the concentration of pigments in Harvey units. These results are presented in slightly altered form in Fig. 20. In the northern zone, where light stops limiting photosynthesis as early as September, the increase in the quantity of algae begins in October; the maximum is reached in December, during the period of sharply increasing stability of the surface layer; in March, the late-summer minimum occurs; in April, a second maximum, significantly less than the December maximum, is observed, followed by a sharp decrease, accompanying the autumnal mixing. From north to south, the length of the period of vegetation decreases, the time of the peak is increasingly delayed (January-February), and the second maximum drops off in the intermediate zone, then disappears completely in the southern zone. The correctness of these concepts, in their general features, has been confirmed repeatedly (Vinogradov, Naumov, 1961; Hasle, 1969; Steyaert, 1973; Voronina, Zadorina, 1974).

Extremely sparse materials are available for the Subantarctic. The vernal maximum of plankton in the Atlantic sector is observed there primarily in October-November (later in the south than in the north); the second peak, apparently, occurs in March-May. In the Pacific Ocean sector, where the boundary of the Subantarctic is shifted far to the south, the bloom is observed in late December (Cassie, 1963; Hasle, 1969).

This picture is quite schematic, and the limits of possible fluctuation of individual indices are great. Among the factors defining the onset of biologic spring (according to Bogorov, 1938), only changes in solar radiation are constant with respect to time. The depth and intensity of the pycnocline depend on the force and duration of the wind (Makerov, 1956); a decrease in temperature may cause ice formation in the high latitudes even in mid-summer;

Fig. 13. Seasonal changes in the stability of the 0-100 meter layer in the northern region of the Antarctic (Currie, 1964).



the configuration of the coastline modifies the drift of the ice, causing its accumulation on the eastern sides of projecting parts of the coast, and milder conditions on their western sides (Yeskin, 1969); the specifics of the edge of the shelf and of the deep water circulation lead to the fact that in some places the southern waters become free of ice earlier than the more northern. All these peculiarities disrupt the latitudinal sequence of the hydrologic and biologic seasons. Along with the main seasonal maxima of phytoplankton, other maxima may exist, e.g., at the edge of the ice or near icebergs (Kozlova, 1964; Steyaert, 1973; Voronina, Zadorina, 1974). The time of the bloom may change from year to year in the same place. For example, at 20°E in January of 1967, the maximum population of diatoms was located some 6° further north than in January of 1965. Such deviations make the average picture of seasonal changes in the quantity of phytoplankton smoother; therefore, in order to judge the true amplitude, measurements must be made during the extreme periods. There are little data suitable for comparison, due to the great variety of methods which have been used for collection and processing of phytoplankton and for the presentation of results. Therefore, here and below, in order to describe the quantity of phytoplankton, in addition to the number of cells, we will also use information on plant pigments, and--at times--on primary production.

In the winter, beneath the ice, there are practically no algae. In the open water in the Antarctic, the concentration of plant pigments is about 50 Harvey units per cubic meter, the mean monthly quantity of chlorophyll "a" at the surface is not over 0.1 mg/m^3, decreasing in places to 0.01 mg/m^3 (El-Sayed, 1970a). During the period of the phytoplankton bloom in the Antarctic waters, the number of diatoms at the surface reaches 1-4·10^5, and even 10^6 indiv./liter (Fukase, 1962; Zernova, 1970; Steyaert, 1973; Marumo, 1957; Kozlova, 1964). The mean number of algae in the upper 100 meter layer is on the order of 10^4-10^5 indiv./liter (Sanina, 1963; Steyaert, 1973). The concentration of plant pigments during this time may exceed 5·10^4 Harvey units per cubic meter (Hart, 1942); the concentration of chlorophyll "a" exceeds 15, reaching 123 mg/m^3 (El-Sayed, 1968a, 1970a, b); the biomass of wet seston, strongly dominated by phytoplankton, may reach 27 g/m^3 (A. I. Ivanov, 1959) and 66.5 cm^3/m^3 (Marumo, 1953). Even beneath non-thawing ice, at the time of breakup of its lower surface, the population of the Phaeocystis reaches 1 million cells/liter (Bunt, 1964b). In the Subantarctic at 20°E, during the bloom, the population of diatoms in the upper 100 meter layer has been observed as high as 3.4·10^5 cells/liter (Steyaert, 1973), to the southeast of the Falkland Islands--1.5·10^7 cells/liter.

These data show that the scale of time changes in the quantity of phytoplankton is very great. Unfortunately, there are but limited materials available for a judgment concerning the length of the maximum period. In the coastal waters near the Southern Orkney Islands, the time of maintenance of high concentration of chlorophyll "a" is about 3 weeks and the high indices of primary production last for about 2 weeks (Horne et al., 1969), while in the area of Mirnyy, the duration of the period of intensive production was less than 10 days (Klyashtorin, 1964). All of this indicates the very short duration of the periods of high concentration of phytoplankton. The drop in phytoplankton occurs during the period with a high content of nutrients in the water, and cannot be explained by exhaustion of them. Probably, the reason for the phytoplankton drop is the increased consumption of algae by the developing generations of herbivores (Hart, 1942; El-Sayed, 1968b; Horne et al., 1969). However, no comparison of the rates of production and consumption has ever been performed; the content of trace elements and vitamins has never been determined, although the influence of these factors on the development of algae may be very great (Provasoli, 1963; Belser, 1963). Therefore, the concept of the connection between the seasonal decrease of phytoplankton and the press of herbivores is as yet but a hypothesis.

Vertical distribution. During the production period, the maximum of phytoplankton population is located in most cases in the upper 10 or 20 meter layer (Hart, 1942; Hasle, 1969). It lies frequently not at the surface, but rather at a depth of 5-10 m. The quantity of algae decreases more or less rapidly with increasing depth below this layer. Usually, a clear dependence is observed between the degree of the density stratification of the water and that of the phytoplankton (Hasle, 1969). With high stability of the surface layer, the algae are found in the uppermost level, and most of their populations are in the euphotic zone, where illumination is optimal. In the Southern Ocean, where nutrient salts are not limited, we should not expect any negative influence of stability on the production at the end of the season, as occurs in the northern temperate regions (Riley, 1946). With stronger vertical motions of the water, the distribution is more uniform, conditions of photosynthesis deteriorate and the quantity of phytoplankton decreases. This is observed in the area of the Antarctic convergence (El-Sayed et al., 1964; El-Sayed, Mandelli, 1965; Mandelli, 1967) and in places with intensive upwelling of water, e.g., in the region of the cyclone near the divergence to the north of Enderby land (Beklemishev, 1959), but not along the entire zone of the divergence, as has been sometimes thought (Beklemishev, 1960; Kozlova, 1964). The influence of factors facilitating or preventing an increase in productivity of phytoplankton is felt through the influence on its vertical distribution.

In many places, particularly in less stratified water, more than half of the population is found in the hypophotic zone (Mandelli, Burkholder, 1966; Horne et al., 1969; El-Sayed, Dill, 1972). Sometimes even the maximum population is located deeper than the compensation point. This, apparently, is a result of its submergence from the higher levels, and indicates a late stage in the seasonal succession.

Summarized data on the distribution of the population of individual groups of algae are presented in Table 6. The greatest tendency to remain near the surface layer is observed in the flagellates and diatoms. This tendency is significantly less in the dynoflagellates, among which are many obligate heterotrophs, and minimal in the Coccolithophoridae. The distribution is somewhat less clear in the Subantarctic: The surface layer contains a smaller fraction of phytoplankton, the population maxima are located deeper.

Table 6. The frequency of occurrence of the population maxima of various groups of algae (% of number of stations) in different layers in the Pacific sector of the Southern Ocean in December 1947-February 1948 (after Hasle, 1969).

Group	Zone	Depth, m 0-25	26-50	51-75	76-100	>100	Maximum depth
Diatoms	A	72.3	12.5	7.5	7.5	0	98
	SA	65	10	5	0	20	162
Dynoflagellates	A	62.5	27.5	7.5	2.5	0	98
	SA	50	30	15	5	0	76
Monads and Flagellates	A	82.5	12.5	2.5	2.5	0	92
	SA	66.5	28.5	5	0	0	71
Coccolithophoridae	A	50	25	0	25	0	100
	SA	39	11	39	5.5	5.5	182

Note: A = Antarctic; SA = Subantarctic.

Ice flora. The vegetation of algae is possible not only in the open water, but also in the ice. There are two maxima of development of ice phytoplankton: the fall maximum, appearing on the bottom surface of the ice in March-April when the thickness of the ice is about 30 cm, and the spring maximum, arising in October at a depth of more than 1 m (Hoshiai, 1972). The ice flora is usually localized in the water-snow and congelation-ice layers (Oradovskiy, 1973). The composition of diatoms differs in these two layers and, apparently, is determined by the time of settlement. An eponic group is distinguished, including attached species of the genera Pleurosigma, Nitzschia, Amphiprora, Fragilaria, and a permanently planktonic group, living among the ice crystals: Biddulphia, Coscinodiscus, Asteromphalus (Bunt, Wood, 1963). The main group of this algae are diatoms. Their number in this biotope may be very high: up to $5\text{-}40 \cdot 10^6$ cells/l, while under the ice it is extremely low (Bunt, 1963, 1968). The ice community lives under extreme conditions: The content of nutrient salts is lower than in the open water (Oradovskiy, 1973), illumination amounts to only a few hundredths of 1% of the illumination on the surface (Bunt, 1968). Therefore, only forms adapted to weak light can live in the ice. Actually, the algae liberated from the ice manifest the maximum photosynthetic activity at an illumination level of 10^3 lx (Bunt, 1968), 1/10 that of planktonic representatives of the group (Ryther, 1956). This can be reflected in the productivity of the population. Under natural conditions, the time between divisions in diatoms averages 6 days (Bunt, 1968). However, due to the absence of sinking, even with this extremely low development rate, a quite detectable increase in population occurs over the vegetation season. This factor, plus the high content of chlorophyll, resulting from the insufficiency of light, has led several authors to consider the ice flora to be of high significance in the synthesis of organic matter. This is not true. But doubtless, its influence on the pelagic community is quite great. The area of annually thawing ice is some 18 million km^2 (49% of the area of the Antarctic zone). As it breaks up, a tremendous quantity of algae enters the water. Many species become true plankters and continue their existence in the water. This intensive "seeding" of the water area as it opens from the ice is of great ecologic significance, facilitating a rapid onset of the bloom.

Regional differences in the quantity of phytoplankton. Are there differences among regions of the Southern Ocean in terms of abundance of phytoplankton? It is difficult to answer this question, due to the asynchronous appearance of the definite stages of the annual cycle and the briefness of the bloom. A comparison can be made only on the basis of materials collected by the same method, for water areas, the plankton of which is in the identical state of seasonal development, preferably for the period of the maximum or on the basis of multiannual studies. In spite of the limited nature of the available data, some general concepts have been developed with respect to this question.

The neritic regions, both of the Antarctic and of the Subantarctic zones, are richest. The mean abundance of phytoplankton in the 0-100 m layer during the period of the maximum near South Georgia Island is more than 10 times the mean abundance in the remaining water area south of the Antarctic convergence (Hart, 1942). Since this region was among the first studied, information on it was applied to the entire ocean, and the initial estimates of productivity of the Antarctic were thus far too high. Averaging of a large volume of data on Pacific and Atlantic sectors of the Southern Ocean have shown that, on the whole, the neritic waters are approximately 5 times richer than the oceanic waters (El-Sayed, 1970a). The reason for this is the abundance of trace elements and the intensive consumption of phytoplankton more intensive in comparison to the open ocean. Within the oceanic waters of the Antarctic, there are significant differences between the northern and southern zones. Many observations indicate a significant increase in the maximum in the southern latitudes, particularly in the waters near the ice. It is here that record concentrations of algae have been observed (Kozlova, 1964; Walsh, 1969; A.I. Ivanov, 1959; Hasle, 1969). These differences are apparently based on an increase in the stability of the southern waters, caused by thawing, as well as the "seeding" of the pelagic zone by the flora liberated from the ice (Hart, 1934; Bunt, 1964a). Therefore, the boundary of the rich zone should apparently more correctly be considered to be not the Antarctic divergence (Kozlova, 1964), but rather the northern limit of the icepack.

Many authors have affirmed the relatively low quantities of phytoplankton in the Subantarctic zone in comparison to the Antarctic (Boden, 1949; Beklemishev, 1960; Kozlova, 1964; El-Sayed, 1970a). However, some data indicate that inverse quantitative relationships do exist (Hart, 1934; Cassie, 1963; Hasle, 1969; Steyaert, 1973). The quantity of algae during the peak period in the Subantarctic can reach the same order of magnitude as in the lower Antarctic. The opinion of the poorness of the Subantarctic has resulted apart from the fact that this area is usually explored by expeditions which have come in to study the Antarctic summer, and they crossed this zone after the phytoplankton bloom; comparisons have been conducted for waters in different stages of plankton succession.

The data presented reflect the differences in the individual water areas only in terms of the quantity of phytoplankton during the period of abundance. Productivity estimates might be essentially different, first of all due to the different duration of the vegetation season. Attempts to determine this quantity approximately on the basis of the data presented by Hart (1942) on the mean annual quantity of plant pigments show that the southern zone is 20% poorer, the northern zone 20% richer, than the intermediate zone. The inshore waters of South Georgia are four times more productive than the northern zone, within which this island lies.

Composition of flora and its seasonal changes. The flora of the Southern Ocean has been studied quite insufficiently. At the present time, some 180 taxons of diatoms, 70 species of dynoflagellates, five coccolithins and five silicoflagellates have been listed (Hasle, 1969). We can use the data of Hasle (1969), who has considered the area of distribution of 77 species (in addition to the broadly distributed species) to judge the degree of isolation of the flora of individual zones. Among the species she studied, the number found in the Antarctic and Subantarctic is practically the same; 30% of the species inhabit the Antarctic alone; some 27% of the species are not seen in the Antarctic; all of them, except for one Subantarctic endemic species, being invaders from the northern waters. The low degree of endemism of the Subantarctic flora in comparison to the Antarctic also follows from analysis of the distribution of dynoflagellates (Balech, 1968).

A predominant role of diatoms is characteristic for the Southern Ocean. Their number in the Subantarctic represents up to 80%, in the Antarctic up to 99.9% of the species present (Hart, 1934). The composition of phytoplankton is quite uniform: Almost always (96% of cases), one or two species make up more than half of the total population (Marumo, 1953). Among the dominant species are: in the Subantarctic, *Chaetoceros neglectus*, *Nitzschia* "*barkleyi*," *Coccolithus huxleyi*, in the lower Antarctic--*Ch. dichaeta*, *Ch. neglectus*, *Fragilariopsis* "*nana*," *N. closterioides*, in the higher Antarctic--*F. curta*, *F. cylindrus*, and *N. subcurvata*. The variety index of flora (after Margalef) is not great, increasing from 2.4-3.0 in the southern zone of the Antarctic to 3.2-3.7 in the Subantarctic (Hasle, 1969).

The use of the fluorescent microscope in recent years has changed many of our concepts of the composition of phytoplankton in the Southern Ocean. It has been shown that, considering the microflagellates, its total population reaches $1\text{-}5\cdot10^{13}$ indiv./m^2. with nanoplankton making up as much as 99% of the total number of cells (Walsh, 1969). However, the distribution and duration of existence of these concentrations are still not known.

The composition of plankton changes with time. Extensive cruise collections (Hart, 1934) have allowed an attempt to be made to classify the most abundant species in accordance with their seasonal abundance and to distinguish: vernal forms; forms which make up the maximum in the spring, but are retained in large numbers throughout the entire season; species which participate in the formation of the spring and fall maxima, and species which form the maximum in late summer and fall.

Further investigations have resulted in the detection of a succession in species composing the peak during its seasonal shift to the south. In addition to species which are present everywhere, others have been found which are significant only in the northern or only in the southern latitudes (Steyaert, 1974). Forms have been described which increase their number during the decrease in the total quantity of phytoplankton. However, in spite of the great qualitative variety of flora, we should not expect to find a rigid succession of dominant forms, particularly since the degree of connection of certain species of algae with others through the metabolite path varies from obligate symbiosis to complete independence (Lukas, 1964).

Let us emphasize the most important specifics of the phytoplankton of the Southern Ocean: great amplitude of quantitative changes during the course of the year and regional differences in maximum abundance; brevity of the maximum; a general shift in the zone of the bloom during the course of the season from the north to the south; significant local variations in the time of onset of the maximum. related to local hydrologic and meteorologic conditions; a seasonal succession of the composition of the phytoplankton.

4.2 Zoocenes.

Life cycles. The main peculiarity of cold-water ecosystems, the discontinuity of the process of primary production, has its maximum influence on the mode of life of the main groups of animals in the Southern Ocean. The cycles of herbivorous interzonal copepoda of the Antarctic and Subantarctic occur practically identically and consist in successive changes of the physiologic state, abundance, age composition, vertical structure and distribution of the numbers of the populations. During the biologic spring, sexually mature crustaceans accumulate in the narrow surface layer, richest in phytoplankton. Their total number during this period is usually not great, but local concentrations may be significant. They feed, mature and breed here. All representatives of the families Calanidae and Eucalanidae are characterized by a broad feeding spectrum, and in all stages of their development, beginning with the first copepodite stage, they consume all species of algae measuring from 5-300 μm in diameter.

The number of eggs produced by the females is apparently directly dependent on their food supply, i.e., on the quantity of algae present during the spawning season. The buoyancy of the eggs of the copepods is negative, but some excretions of the phytoplankton increase the viscosity of the water and slow the sinking of the eggs (Maloney, Tressler, 1942). The nauplii emerge in the uppermost layers of water and a high concentration of the population, the core of which is usually in the upper portion of the mixing layer, is characteristic for early stages of the development of the generations. The total number of individuals reaches its maximum during this period. Later, as the crustaceans grow, they gradually disperse vertically: The older stages begin to sink into the depths, and at first the lower boundary, then the upper boundary of their habitat move downward. Therefore, in the summer the cores of abundance of individual copepodite stages typically go deeper as they become older (Voronina, 1970a, 1974).

As time passes, the populations are significantly reduced in number, but, due to the intensive growth of the individuals, their total biomass increases, reaching its maximum in the surface layer during the period of dominance of the fourth and fifth copepodite stages. Older stages, having accumulated large droplets of fat, begin to leave the euphotic zone and disperse through the mass of the water. The number maxima of the individual species are observed in the winter at a depth of 750-1000 or 250-750 m (Mackintosh, 1937; Andrews, 1966). The wintering populations of copepods over most of the aquatorium are characterized by predominance of the fourth and fifth copepodite stages. During this period, the crustaceans do not feed and utilize the summer fat reserves. The populations retain the sequence of individual copepodite stages along the vertical of late summer: younger copepodites are located higher than older. However, in spring, as the rise begins, a restructuring of the vertical distribution occurs, since the mature individuals which move more rapidly than the others, catch up with and even pass first and fifth, then the fourth stage copepodites, after which the fifth stage copepodites pass the fourth stage copepodites. As a result, a structure is produced which is typical for the final stages of migration, in which the older stages are followed by younger stages from the top downward. The vertical spread is greatly reduced, reaching its minimum during the spawning period. In general features, the changes in the sequence of copepodite stages along the vertical and of quantitative distribution of species numbers by depth can be represented as in the diagrams below (Figs. 14 and 15). The individual stages of this cycle differ in their age composition and total numbers of populations.

This type of restructuring has been seen for Calanus propinquus, C. simillimus, Calanoides acutus, Rhincalanus gigas, as well as Pareuchaeta antarctica and Metridia gerlachei, in which it is somewhat complicated by the daily vertical migrations. Apparently, these cycles are characteristic of all interzonal copepods which breed in the surface layer.

One important peculiarity of the annual cycles of planktonic animals is the asynchronism in occurrence of identical stages of these cycles in various latitudinal zones. The rise to the surface, breeding, attainment

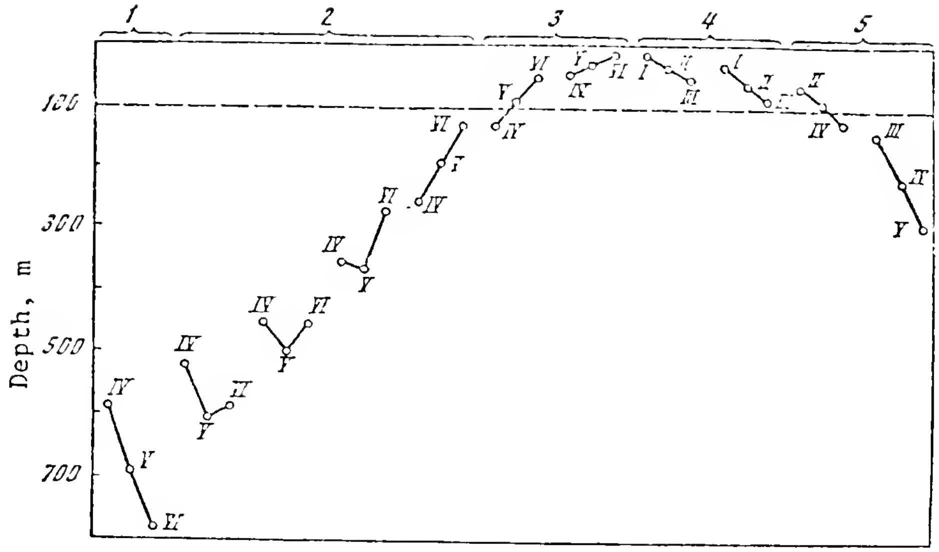


Fig. 14. Changes in vertical structure of population of interzonal species during the annual cycle. Roman numerals show position of median of hemipopulations of individual copepodite stages. 1, Winter; 2, Beginning of spring migration; 3, End of migration, spawning; 4, Development of new generation; and 5, Beginning of fall sinking (Voronina, 1975).

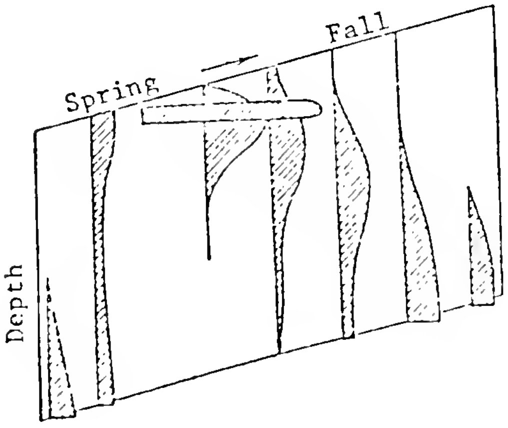


Fig. 15. Seasonal changes in vertical distribution of interzonal species population (Voronina, 1972).

of a certain age, and maximum biomass and the downward migration occur earlier in the northern latitudes and later further south (Voronina, 1969, 1974; Voronina, 1970). Deviations from this sequence are related to hydrologic peculiarities which define the deviations in the time of beginning of intensive phytoplankton production (Voronina, 1975). The time difference of the onset of individual stages may be quite great. For example, in the zone of the Antarctic convergence, the breeding of Calanoides acutus occurs in November, of Rhincalanus gigas--in December, while in the southern latitudes they occur in February and late March, respectively. As a result, as we move along a meridian, we can observe sequential changes in the age and space structure of the populations and their abundance, analogous to their changes with time.

The duration of the cycle differs for different species. Populations of C. acutus and C. propinquus follow a single generation almost everywhere; R. gigas in the southern latitudes, with the short vegetation season, does not succeed in completing its development in a single summer, and it is extended over two years (Voronina, 1970). The Subantarctic C. similis and C. tonsus, apparently, are bicyclic. The specific differences in the development of copepoda primarily concern the time of the spring ascent to the surface and breeding, as well as certain details of the vertical distribution: depth inhabited by the wintering group, absence or presence of daily migrations and their scale.

Another important group of the pelagic population is the euphausiids. The cycle of the most numerous species of this group, Euphausia superba, living south of the Antarctic convergence, has been most fully studied. This crustacean, apparently, can breed in any region of the Antarctic where spawning accumulations are formed, even around South Georgia Island (Mackintosh, 1972; Makarov, 1972). The eggs are spawned in the upper layers, then gradually submerge to great depth, as much as 2000-3000 m (Fraser, 1936; Bargmann, 1945; Marr, 1962). During the sinking their cleavage proceeds. As a result the deeper the eggs, the more advanced is their development. The emerging nauplii begin active ascent during which development continues. The larvae usually reach the surface water in the first calyptopis stage. Only here do they begin active feeding. The morphogenesis of E. superba is very variable (Fraser, 1936). Five different paths of ontogenesis of the crustaceans have been described. The path followed by development is apparently determined by the environmental conditions (Makarov, 1974).

In the surface water the larvae perform vertical migrations, the amplitudes of which decrease with increasing age (Marr, 1962). However, simultaneously with this, the entire population tends to rise and is concentrated in the upper 25 or 50 meters of water (Makarov, 1974). The seasonal submergence into the deep water does not occur for this species. The biologic sense of this cycle is obvious: The submergence of the eggs and early larvae below the layer where they can be eaten by mature euphausiids helps to preserve the population (Marr, 1962; Pavlov, 1969). During the first year of life, the crustaceans complete their larval phase of development;;during the second year the juveniles feed and grow; during the third year, the crustaceans mature and breed. In case of unfavorable conditions, the cycle can extend to four years; this is characteristic of crustaceans in the most southern Antarctic regions (Makarov, 1972).

Varying their location in the great range of depths, E. superba is subject to the influence of various hydrologic factors which, to a significant extent, determine the character of its distribution in various developmental stages. The early larval stages of this species, in contrast to the mature stages, occur in a rather limited water area, including the East Wind Drift and the Weddell Sea circulation. No other of the numerous species of the Antarctic have such distribution. All other biologic boundaries in the pelagic zone coincide with the zones of physical boundaries or are parallel to them. The picture of the quantitative distribution of _E. superba_, however, shows clear asymmetry and brings up the question: What prevents the development of the larvae over the broad aquatorium of the West Wind Drift in the Indian and Pacific Ocean sectors, the ecologic conditions in which are practically the same as those in the Atlantic? At the present time, this factor has but one explanation. Obviously, the depth of submergence of the eggs and, consequently, the distances which the larvae must travel as they rise to the phytoplankton-rich waters, are different in different regions and are inversely dependent upon the density of the water. In the shelf zone, filled with cold water, submergence occurs more slowly, and even if the eggs fall to the bottom, the larvae emerge in lesser depths and come to the surface in earlier stages than in the oceanic zone (Marr, 1962). We can assume that there is a depth limit which the nonfeeding larvae can travel on their return path upward, and that individuals which descend to greater depths die without reaching the layer of photosynthesis (Voronina, 1974).

Obviously, the vertical structure of the water has a very significant influence on the depth of submergence of the eggs; in particular, the transition from the deep water mass to the denser bottom water should be accompanied by a slowing or complete stoppage of movement, as is observed in the sinking diatoms (Wood, Walsh, 1968). A comparison of the topography of the upper boundary of the bottom water mass and the quantitative distribution of the calyptopes of _E. superba_ has yielded interesting results. The Antarctic bottom water mass is formed as a result of cooling and freezing of shelf water with its subsequent mixing with the deep water and sliding downward along the slope (Mosby, 1934). Therefore, the depth of its upper boundary increases rapidly from the continent to the north. Only in the Weddell Sea is there a dome-shaped elevation of this water, caused by the cyclonic circulation (Klepikov, 1963). It has been found that the location of the calyptopes practically coincides with the zone where the denser water lies at a comparatively shallow depth--around 1800 m. This depth corresponds approximately to the maximum depth of winter sinking of the interzonal copepoda and, probably, is close to the maximum distance which many interzonal organisms can travel in their seasonal vertical migrations. This gives us reason to believe that the breeding of _E. superba_ can be truly successful only in regions where the upper boundary of the bottom water mass is located relatively high. In this area there are two large circulations (the East Wind Drift and the Weddell Sea circulation), holding most of the rising crustaceans within their boundaries. Therefore, the maximum population of all stages is found in these waters, and only a portion of the population is carried out beyond them. The process of gradual expansion of the habitat as the generation develops has been clearly traced (Fig. 16) in larvae living in the surface layer: The boundaries of their distribution shift to the east from month to month (Marr, 1962).

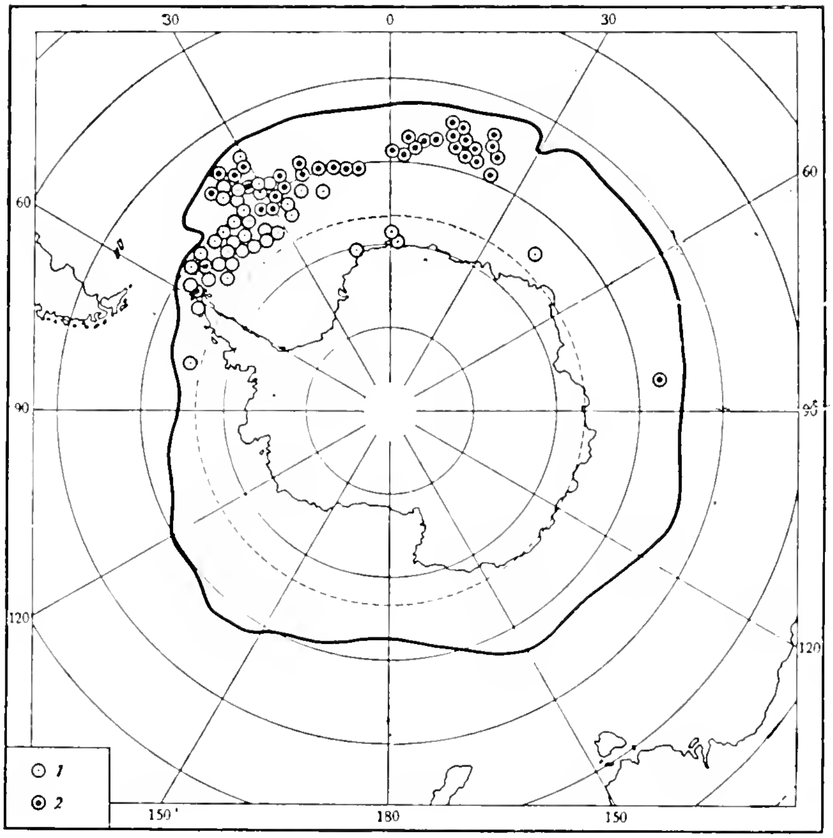


Fig. 16. Distribution of larvae of *Euphausia superba* on the surface. 1, Summer; 2, Winter (Marr, 1962, simplified).

Expatriation to the north, to South Georgia Island, occurs both as a result of direct penetration of water from the Weddell Sea with the current flowing along the arc of the South Sandwich Island, and as a result of episodic transfer of surface water through its boundary zone (Solyankin, 1969; Maslennikov et al., 1971; Yelizarov et al., 1973). The transfer of crustaceans from the East Wind Drift is possible in areas where the branches of the circulations which form it turn to the north (Treshnikov, 1964). The movement of the surface water in this direction has been described on the basis of satellite observations of iceberg drift (Tchernia, 1974). As a result, a portion of the population of *E. superba* is scattered over the broad spaces of the Antarctic beyond the limits of its main area of distribution. Such representation agrees well with materials on the quantitative distribution of krill (Marr, 1956, 1962): Massive accumulations of crustaceans are related to the East Wind Drift, the circulation of waters of the Weddell Sea, regions of Bransfield Strait and South Georgia Island, i.e., they are similar to the distribution of calyptopes, but somewhat broader. New data (Mackintosh, 1973) have not carried us beyond the framework of this

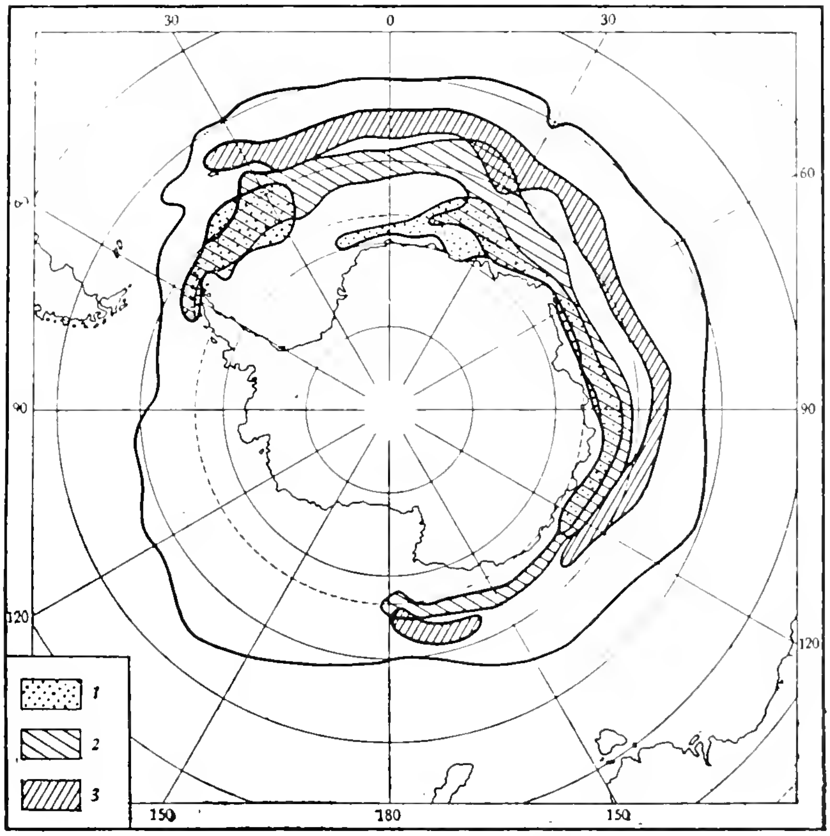


Fig. 17. Change in the position of the regions of commercial whaling during the course of the summer (according to pre-war data). 1, November; 2, January; 3, March (Mackintosh, 1973, modified).

concept. A slightly different picture is yielded by the summarization of multiannual visual registrations of surface swarms, undertaken by Mackintosh, according to which the "krill zone" is a narrow circumpolar ring, moving southward in the summer, following the retreating ice. Its furthest northern position is observed in December, its most southern position--in March. It agrees well with the distribution of commercial accumulations of whales (Fig. 17); therefore, the disappearance of swarms in the northern latitudes is related by this author to consumption. However, E. superba swarms in the intervals between feeding and the existence of swarms is longer, the more abundant the phytoplankton; i.e., the presence of swarms is most typical of the period of phytoplankton bloom (Pavlov, 1969, 1974). The position of the phytoplankton maxima ring, as shown above, changes with time analogously to the zone of krill swarming. This indicates that the picture drawn by Mackintosh is primarily a reflection of the character of distribution of E. superba and can hardly be considered as an indication of the abundance of the species, although, in principle, there is doubtless a decrease in the abundance of the crustaceans in feeding zones.

The peculiarities of the biology of other Antarctic and, particularly, Subantarctic euphausiids have been much less thoroughly studied. The second most massive species is Thysanoessa macrura, widespread in the Antarctic and extending into the southern Subantarctic. Judging from the occurrence of the early stages, breeding of this species occurs between October and February, the duration of the cycle being one year (Ruud, 1932; Rustad, 1934; K. N. Pertsova, 1975). The population maximum is found in the upper 100 meter layer. The regions of greatest abundance of both mature individuals and larvae are extended along the Antarctic convergence and divergence (Lomakina, 1964; K. N. Pertsova, 1975). Euphausia triacantha has a similar distribution, but the primary concentrations of this species are clearly confined to the convergence zone (Baker, 1959). This species performs great diurnal migrations, submerging during the day to depths of over 250 m, and has a two-year cycle. The duration of life of E. frigida is the same.

The third important group of herbivores is the salps. Of these, the cycle of Salpa thompsoni has been most thoroughly studied (Foxton, 1966). It is very common to the south of the Subtropical convergence. The range of habitat extends down to 1500 m, the maximum population being found in the surface water. There are daily migrations. During the course of the winter, the juvenile asexual forms grow, developing stolons which carry the buds of sexual zooids. Early in the spring, the fully formed sections of the stolons begin to separate. From October through February, their number increases by a factor of more than 10, but then decreases once more in March. As the colonies grow, they submerge into deeper water. In each, one fertilized egg develops which, after completing morphogenesis, is liberated at the end of the summer and continues to develop in the form of an individual, supplied with a food reserve and already having a primordial stolon. The development of the salps in the deep layers occurs more slowly and by the beginning of spring, some individuals are still in the early stages of development. Therefore, throughout the summer the population consists of organisms of varying ages.

The most numerous group of predators--the chaetognatha--is also interzonal. Most abundant are Eukrohnia hamata, Sagitta gazellae and S. marri. The annual cycle is best known for S. gazellae (David, 1955). Breeding occurs in the deep zone from spring to fall. The region of its greatest intensity shifts as the season progresses from the northern Subantarctic to the south. The spawned eggs float into the upper horizons: Hatching occurs at a depth of about 250 m, subsequent development--in the 0-100 m layer. In the winter, the Sagitta grow by approximately 5 mm per month, somewhat more rapidly in the spring and summer. Juveniles, as they mature, gradually submerge, the more mature individuals being located deeper. Mature individuals are found only at depths of 1000-1500 m. The duration of one generation is one year. The development of other species differs only in details. All species perform seasonal migrations.

The predaceous Hyperiidea Parathemisto gaudichaudi begin to breed in September. Each female spawns several times, after which some of the females die, while others survive to the fall and breed again. The juveniles appear in September, reaching their maximum number in December. Due to the long period of breeding, the young crustaceans are present in the plankton as late as June. Some of the larger females may survive a second winter and breed again (Kane, 1966).

A comparison of the mode of life of the most numerous plankters shows great similarity with respect to the most important characteristics: Breeding (or the time of its maximum intensity) in all species occurs in the spring or summer; feeding and growth of the juveniles occur in the surface or subsurface layer; most of the population perform daily, seasonal and/or ontogenetic vertical migrations, removing them from the surface waters.

This similarity of cycles in different groups of organisms is a result of the peculiarities of the environmental conditions in the Southern Ocean. The discontinuity of the process of primary production makes it necessary for numerous species to spend the vegetation season in the euphotic layer or directly beneath it. Here, the herbivores find the maximum algae and can grow rapidly, breed and create reserves of fat for the long winter, while the predators feed on the concentrations of copepoda and euphausiid larvae. However, if the entire life cycle were spent in the surface waters, there would be the danger of loss of a significant portion of the population by being carried by meridional currents away from the breeding zone. Any vertical migration decreases the effect of this transfer, while scattering into the deeper water makes it harder for predators to decimate the population. The specifics of the biotope have resulted in the predominance in the zoocene of the cold-water pelagic zone of nonspecialized interzonal species, occupying "large" niches in comparison to those of the tropical plankters.

Another important feature of the life cycle of the zooplankters is their great plasticity. This is manifested as the variable duration of development of different individuals (P. gaudichaudi, R. gigas, E. superba), as well as the mixed age composition of populations (Salpa thompsoni, P. gaudichaudi), and the variety of possible paths of morphogenesis (E. superba). The plasticity of cycles allows the species, depending on environmental changes, to change their development, which serves as a sort of insurance in case of excessively severe perturbations.

The differences between cycles consist in the greater length of the breeding period of most predators in comparison with the existence of high concentrations of their prey. The time of breeding and the range of vertical distribution is also diverse in various species. At first glance, these differences seem to be secondary in nature but, as will be demonstrated below, they are of primary significance for the structure and functioning of the community.

The quantitative distribution of individual species is influenced by a variety of factors, among which we can distinguish two important groups: temporal and regional. The amplitude of fluctuations in the number of individual populations during the course of the year may be very significant. It is particularly great for plankters with nonoverlapping generations, including all of the interzonal copepods. The numbers of the new generation are maximal after hatching. Subsequently, their number decreases due to consumption and natural death. At the same time, as the juveniles develop, the relative fraction of older individuals increases. On the average, during the time of the development of the population from the stage of domination of early copepodites to domination of the fourth or fifth stage, the number of crustaceans beneath each square meter decreases by a factor of three or four, then still more sharply over the next winter. It follows from this that, in addition to the regional aspects of distribution, any survey reflects the seasonal aspects, the differences resulting from disagreement in phases of the cycle overlapping with local differences. This is important to consider in any comparative evaluation of the abundance of a given species in various latitudinal zones or areas with different ice regimes. A comparison of areas with identical age composition of individual mass species shows that the number of crustaceans may vary by a factor of more than 20, creating a rather variegated picture. It is based upon factors determining their distribution. The former include the number of organisms in the spawning pool and the feeding conditions during the period of breeding and growth. The distribution of the spawning pool of interzonal animals depends on the abundance of individuals of the previous year's generation, descending from the surface waters, and on their subsequent transport by deep water currents. Since the rate of transport by deep water currents is slow, it usually results in no significant changes. Data on the distribution of Calanoides acutus (Andrews, 1966) and the total biomass of zooplankton (Foxton, 1956) shows that the character of distribution remains practically unchanged during the course of the winter months. Only in the central Atlantic sector, where the deep waters, compensating for the great efflux of bottom water, have an elevated southern component in their velocity vector (Arsen'yev et al., 1975), is significant southward shift of the wintering pool of plankters, as well as penetration of subtropical species far into the Subantarctic, and of Subantarctic species into the Antarctic, possible (Andriyashev et al., 1973; Voronina, 1975). In addition to this, some changes in the deep water plankton occur in the zones of divergence, to which the meridional components of the currents "carry" the animals from the nearby water areas. Although these currents are weak, over the course of the long winter, the concentration may increase significantly in comparison with neighboring sections (Voronina, 1966b). In general, the abundance of the wintering pool varies less than the abundance of summer population (Voronina, 1975).

The amount of food available for the ascending plankters depends on the coincidence between the time when the main mass of the population rises to the surface and the beginning of phytoplankton bloom which, as was shown above, varies over rather broad limits. Therefore, in early spring, in some localities we may find older copepodites which have already risen, but because of food absence, cannot moult and begin breeding, whereas in neighboring areas, where the bloom has occurred, many juveniles are already present. Since the regional differences in the time of occurrence of the bloom are determined primarily by the development of the summer density stratification of the water it is this factor which is most important in determining the trophic conditions during the spawning period.

However, various species do not reach the surface and breed simultaneously, but rather in a strictly defined succession. For example, among the copepods in the Antarctic, the earliest species is C. acutus, followed by C. propinquus, then R. gigas (Voronina, 1966a). Therefore, in various places of the area either one or another species is in optimal conditions and yields the greatest brood. These factors are responsible for the changes in abundance of each of the species within the limits of its area of distribution, and the variation in the quantitative relationships between different species. Illustrations of this can be found in materials from the expeditions of the DISCOVERY (Baker, 1959) and OB' (Voronina, 1966b).

In some cases, the influence of the hydrologic structure of the waters is manifested differently. During the spring migration, great hydrologic gradients may prevent the spawning pool from rising into the productive layer, and then breeding occurs in the subsurface waters poor in phytoplankton. This has a sharp influence on the abundance of the brood (Voronina, 1970a).

These are the main factors determining the regional distribution of the abundance of new generations of plankters. The distribution is subsequently transformed under the influence of the currents. The primary significance is the meridional transfer. The transverse studied (Deacon, 1937; B. G. Neyman, 1968; Arsen'yev et al., 1975). The Antarctic surface water with its population moves northward at a mean speed of 5-20 cm/s (in the Subantarctic, somewhat more slowly). In the zones of the Antarctic and Subantarctic convergences, the surface waters move downward, but the organisms remain at their natural depths. As a result, in these narrow zones there is a continuous increase in the abundance of zooplankton due to the influx of allochthonous material. The rate of this increase in one transect through the Antarctic convergence has been found to amount to 3% per day (Voronina, 1968).

The influence of currents on the distribution of various species depends on the time spent by their populations in the corresponding waters. For example, for Euphausia triacantha, which has a two-year life cycle, inhabiting the surface water and, apparently, performing only slight seasonal migrations, the peak at the Antarctic convergence is quite clearly expressed (Baker, 1959), while for the one-year interzonal copepods it is less clearly expressed, although it is still quite clear. For inhabitants of the middle depths, e.g., Sagitta gazellae, on the other hand, a great decrease in the population along the convergence is characteristic, apparently related to the moving apart of their biotope by the descending surface water. The descending layer has so thoroughly disjoined these animals that it has facilitated the formation of isolated populations on either side of the zone of convergence, which have developed into independent races.

The influence of the zone of Antarctic divergence is significantly weaker, and changes from season to season. In the winter, relatively rich plankton accumulates here, yielding the maximum spawning pool. Numerous juveniles appear in spring, moving northward with the surface water, forming easily visible "spots" (Voronina, 1968). The divergence influences the distribution of various species differently. Among the mass copepods, the greatest concentrations are observed for R. gigas, apparently due to the fact that it spends the winter in the higher layers, where the velocities of the currents are greater than in those inhabited by C. acutus and C. propinquus.

Let us sum up our information on zoocenes. Their basic specifics are: low specialization of the most numerous species: absence of any attachment to definite depths or water masses, broad feeding spectra; relationship of periods of breeding and feeding of juveniles to periods of abundant phytoplankton, as a result of which most species in the Antarctic are monocyclic, in the Subantarctic, apparently, bicyclic; significant plasticity of the life cycles; a delay in identical stages of cycles in the southern latitudes in comparison to the northern latitudes; complexity of the picture of quantitative distribution of individual species, depending on both temporal and local factors.

4.3 Communities.

Specific and trophic structure. The number of species in the pelagic zone of the Subantarctic, and particularly the Antarctic, waters is significantly less than in the tropics. Why is this?

The biotopic variety in the temperate and polar waters in the summer, is no less than in the tropics. There are: surface film, an upper mixed layer, a residual layer of winter cooling and two thermoclines separating it from the waters above and below. However, the autumnal mixing disrupts this stratification, and the time of its vernal restoration is variable. As a result, ascending populations, at the same time but at different places, may encounter completely different situations: from complete homothermy of the surface water mass to well-developed stratification, from winter shortage of algae to rather abundant bloom. This factor, apparently, greatly hinders the adaptation of the fauna to the specific conditions of existence. As a result, neither food specialization of herbivores, i.e., adaptation to individual stages of succession of phytoplankton, nor spatial divergence occurs. As a result of this, the variety of species in the population is not great. The relationship between low specific variety of communities and unpredictability of temporal changes in the environment is well known (Margalef, 1968; Slobodkin, Sanders, 1969). For the pelagic zone, where the primary consumers of phytoplankton are located beyond the producing layer for a long time, this factor should have particularly great significance. Another factor in the low variety of the population of the higher latitudes may be the brevity of the period of vegetation of the algae (Heinrich, 1962). In the plankton of the Southern Ocean, phytophagous forms are clearly dominant, their biomass in the upper 100 meter layer representing an average of 82%, in places as much as 96% of the total. The zoophagous animals, the prey of which do not form such abundant concentrations as the phytoplankton, cannot, under the sharply variable environmental conditions, be very productive. The absence of the strong pressure of predators, in turn, may help to maintain the low level of specific variety (Paine, 1966).

All of this shows the great length of the chain of results which follows from the basic peculiarity of the biotopes of the temperate and polar latitudes--the seasonal change in solar radiation. First of all, it assures that the production process is discontinuous, which in turn defines the basic features of the zoocenes: the character of their annual cycles, the level of specific variety, their trophic structure. Therefore, the seasonal changes in solar radiation can be considered the most important factor determining the peculiarities of cold-water ecosystems.

The trophic web. The structure of the trophic web of the Southern Ocean is relatively simple. The phytoplankton is consumed by copepods, euphausiids and tunicata. All of these are nonselective filter feeders. The copepods and euphausiids are consumed by the hyperiids, chaetognaths, predaceous copepods, squids, fishes and baleen whales. The fishes and whales also consume amphipods. The fishes and squids are consumed by the sperm whales and small toothed whales. A definite role in the consumption of the pelagic fauna is also played by the pinnipedes: the crab-eating seal feeds almost exclusively on krill, the other seals--on cephalopods and fishes. Only the Bagridae and sea leopard attack homoiotherms in the Antarctic.

All of these food chains are of the grazing type. The significance of detrital chains, which begin with the utilization of dead organic matter, as well as heterotrophic bacteria in the Antarctic and Subantarctic, is very low.

This trophic web consists of four main levels: producers, phytophages, and first and second order predators. The baleen whales, fishes and marine birds, which consume the phytophages and small predators, occupy an intermediate position between the last two levels. Unfortunately, this system has no quantitative characteristics, since the production, and even the biomass, of many groups of organisms, are as yet unknown. Only approximate data can be presented. The most realistic figures seem to be as follows. The mean annual biomass of net plankton (mesoplankton) in the Antarctic in the 0-1000 m layer is 26 mg/m^2 (Foxton, 1956), while in the period of the summer maximum, in the upper 100 meter layer, in the Indian and Pacific Ocean sectors it reaches 10-20 g/m^2 (Voronina, 1966b). The greatest mass is that of the copepods (73%), followed by the chaetognaths (10%) and euphausiids (8%) (Voronina, 1966c). The biomass of euphausiids, according to trawl data, is about 0.7 g/m^2 (Dolzhenkov, 1975), and in regions of their greatest abundance--up to 30 g/m^2 (Marr, 1962). The biomass of whales during the period of their abundance was 0.56 g/m^2, their consumption of plankton over the summer season about 10 g/m^2 (Nemoto, 1968; Mackintosh, 1973).

At the present time, a radical restructuring of the quantitative relationships between individual elements in this web is occurring.

As a result of intensive hunting of whales, their initial numbers have been reduced over the past 40 years by 85-90% (Mackintosh, 1970), correspondingly decreasing the consumption of their prey. Let us attempt to discuss the results of these changes on the example of E. superba. We could hardly expect that the increase in its quantity, estimated as 30 million tons (Mackintosh, 1970), would cause an increase in the population of its other consumers, since many of them are also intensively fished. It is more probable to assume that self-regulation of the population occurs. The increase in the abundance of krill results in an increase in the intensity of consumption of phytoplankton and a deterioration in the food supply for the individuals in the population. We can assume that, as a result of this, a significant portion of the population will go over, as in the southern waters where food is scarce, to a four-year cycle. Later maturation will result in a decrease in the population of the spawning pool.

Since the crustaceans will live longer, they will drift further north. The zone of their occurrence will expand, but, due to mechanical factors, will remain within the Antarctic zone. Mackintosh has already reported unusual northern occurrence of swarms of E. superba (1973). The transportation of mature crustaceans outside the zone of optimal conditions for the larvae may also lead to a decrease in the abundance of this species.

Spatial structure. The pelagic community has a certain spatial structure, changing regularly with the course of the biologic seasons. The nature of these changes can be considered on the example of the three most numerous species of copepods--Calanoides acutus, Calanus propinquus and Rhincalanus gigas. During the biologic spring, all three species are present as the overwintered population or, in the case of the two former species, early juveniles of the new generation. During this time, the core of the population of C. acutus is located higher in the water and its concentration is at its maximum. The core of C. propinquus is located more deeply, that of R. gigas--deeper still. The spread of the first of these three species may differ, that of the second is always great. This structure results from the fact that C. acutus rises to the surface and forms prespawning accumulations earlier than C. propinquus, and much earlier than R. gigas. Later, when the populations of all three species are in a more advanced state, C. propinquus with characteristic domination by egg-bearing females and the first copepodite stages, for which the surface maximum is typical, takes up the "feeding" position. At this time, the population of C. acutus, in which the second and third copepodites predominate and the fourth copepodites are beginning to appear, begins to descend into the lower layers of the epipelagic zone, while R. gigas, which has not yet completed its spring migration, is still deeper than the other two species. At the end of the vegetative season, C. acutus almost completely leaves the euphotic zone, R. gigas takes up the uppermost position, except in regions where the sharp seasonal thermocline prevents them from rising. In the last case C. propinquus occupies the highest position (Voronina, 1972).

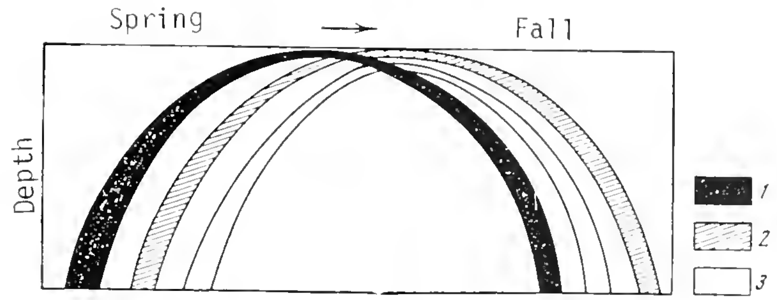


Fig. [illegible] Seasonal changes in vertical structure of a community. The diagram shows the positions and spread of the core of the populations of Calanoides acutus (1), Calanus propinquus (2), and Rhincalanus gigas (3) (Voronina, 1972).

This cycle is illustrated schematically in Fig. 18. This restructuring of the vertical distribution of plankters during the course of the vegetation season occurs at every point in the water area. It is based on the changes in the vertical structure of the populations and the asynchronism of their life cycles described earlier. The earlier occurrence of each phase of the cycle in the northern latitudes, in comparison to the southern latitudes, means that the same sequence of structures will be observed along a single meridian as we move from south to north.

The maxima of biomass of these species is observed in different places in space as a result of the asynchronism of the periods of dominance of the fourth and fifth copepodite stages in the various populations. (During the period of dominance of these stages the greatest biomass concentration is achieved.) As a result, the summer maximum of C. acutus is always located further south or deeper in the water than that of C. propinquus, while that of R. gigas is further north than that of the other two species (Fig. 19). A similar divergence of the biomass maxima has been observed in Subantarctic copepods.

The spatial distribution of locations of maximum concentrations of various species is also characteristic for chaetognaths (David, 1958, 1965) and euphausiids. Apparently, here also, it is determined by the asynchronism in the life cycles (Timonin, 1968). In this manner, competitive interrelationships between similar species are minimized.

The annual cycle in the pelagic zone. The cycles of individual populations, partially overlapping in time, combine to make up the seasonal changes in the total quantity of zooplankton. The quantity of zooplankton in the upper 100 meter layer is characterized (Fig. 20) by two maxima over the course of the year (Foxton, 1956; Voronina, 1970a, b). The first, smaller, maximum is related to the spring ascendance of organisms into the euphotic layer; the second to the development of new

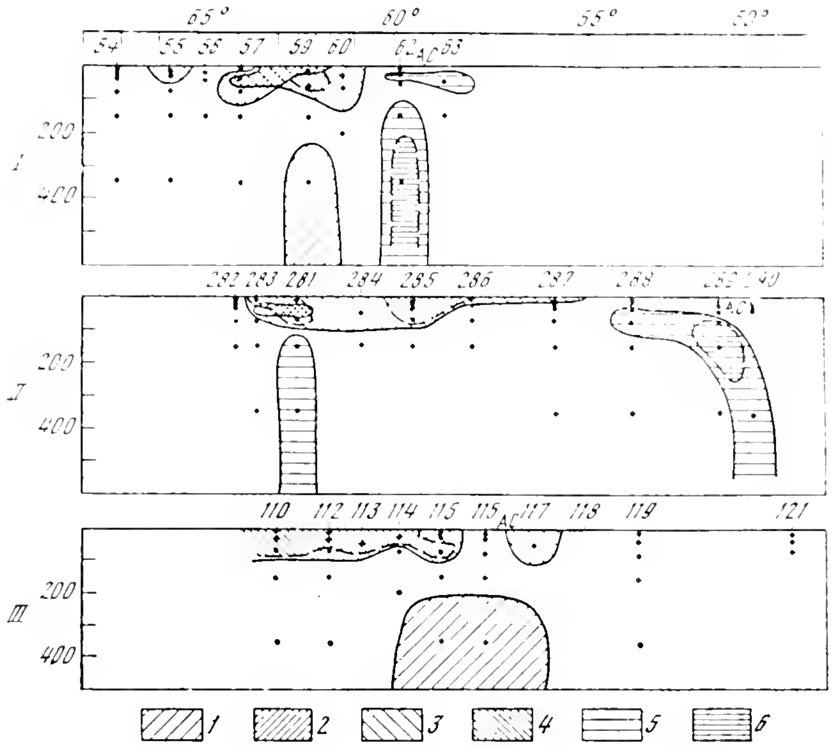


Fig. 19. Position of maxima of biomass of various species of copepods according to collections from the research vessel OB'. I, Cross section south of New Zealand, March-April 1956; II, Cross section along 98½E, April 1957; III, Cross section from Mirniy to Aden, May 1956; AC, Antarctic Convergence; 1, Calanoides cutis >25 mg/m^3; 2, Calanoides acutus, >50 mg/m^3; 3, Calanus propinquus, >25 mg/m^3; 4, Calanus propinquus, >50 mg/m^3; 5, Rhincalanus gigas, >25 mg/m^3; 6, Rhincalanus gigas, >50 mg/m^3 (Voronina, 1970).

generations. The spring migration occurs over a large portion of the water area in a rather short time, but is delayed in the south. The summer maximum is observed in the northern zone in February, in the intermediate and southern zone--in March. Thus, it occurs in the northern and middle zone two months later than the maximum of phytoplankton. The reason for this delay is that the comparatively small overwintered populations of copepods underutilizes the primary production and does not prevent the phytoplankton bloom. Only after breeding and growth of the new generation does effective consumption of algae begin, achieving a balance that is rapidly followed by overutilization which, in the opinion of many researchers, is the main reason for the seasonal drop in the abundance of phytoplankton. At this time (in April), individual planktonic animals begin to leave the euphotic zone, causing a decrease in biomass. In the northern zone, conditions are still favorable for the vegetation of phytoplankton, and the decrease in consumption leads

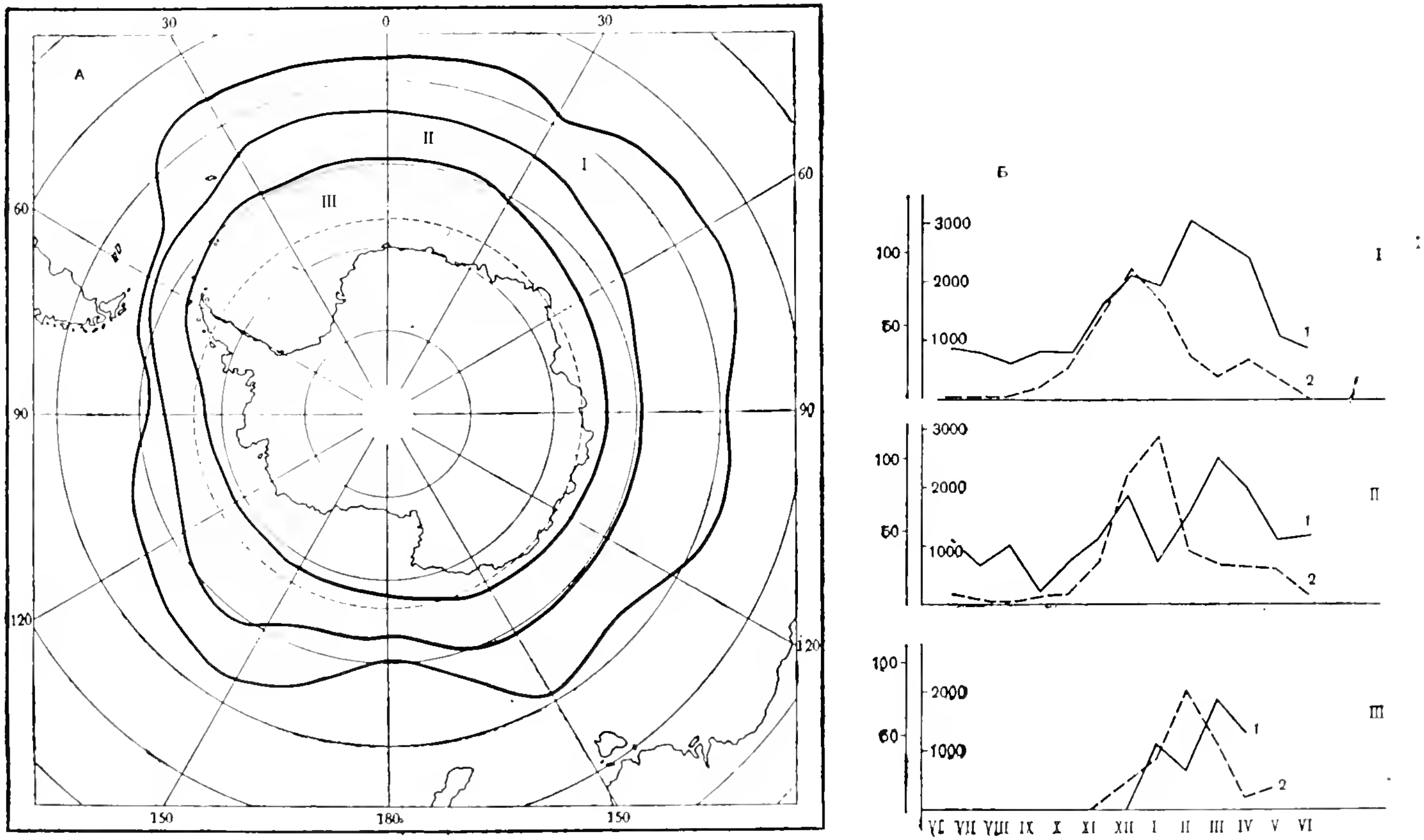


Fig. 20. Seasonal changes in abundance of phytoplankton and zooplankton in the Antarctic. A, Latitudinal zones (Voronina, 1970); B, Mean biomass of zooplankton in 0-100 m zone (after Foxton, 1956) (1) and mean concentration of plant pigments in Harvey units (after Hart, 1942) (2) in these zones.

to a small autumn peak. After the breakup of the seasonal pycnocline, the winter impoverishment of the epipelagic zone begins.

In the extreme south, the maximum of zooplankton lags behind the maximum of phytoplankton by only a month. This is not a result of more rapid development of the zooplankton. The reason is that the early onset of winter causes earlier descent of plankters from the surface waters. As a result, some species do not succeed in completing their development and descend at younger stages.

The difference in time of onset of the maxima for plants and animals is reflected in their spatial distribution as well. The ring of phytoplankton bloom is always located further south than the ring of the summer maximum biomass of zooplankton (Voronina, 1970a, b). In the period preceding the peak of the zooplankton, the maximum concentrations of both groups of organisms usually coincide in the upper layer of the epipelagic zone. Later, they diverge: First, as a result of the overutilization of phytoplankton, its absolute maximum shifts deeper than the maximum of its consumers; at the end of the season, most of the mass of animals descends into the subsurface layer, while the maximum of algae remains nearer the surface.

The great amplitude of fluctuations in the population of algae and the long period of underutilization of the primary production are characteristics of the low degree of balance in the cycles of phytoplankton and zooplankton in the Antarctic. However, the degree of imbalance apparently experiences significant local fluctuations, depending on the hydrologic specifics and the composition of the zooplankton. Wherever, due to a sharp thermocline, the copepods of the winter pool cannot reach the productive layer (Voronina, 1970a, 1974), primary production is still more underutilized than elsewhere. The situation is quite different at the Antarctic Convergence, where the descent of the water decreases primary production, but the quantity of zooplankton increases due to the arrival of allochthonic material. As a result, the ratio of biomasses of phytoplankton and phytophages is significantly lower here than in other areas and, correspondingly, the degree of its utilization increases. The maximum balance for the Antarctic is achieved in waters where the plankton is dominated by euphausiids, particularly _E. superba_, which do not perform seasonal migrations (Voronina, 1970a, b). These large crustaceans, in the post-larval period, are constantly present in the surface water mass and, immediately after the beginning of vegetation, can consume the primary production.

Such is the annual cycle in the Antarctic pelagic zone. The data for the Subantarctic are too sparse, and can be utilized only for a brief description. The occurrence of great seasonal fluctuations in the quantity of phytoplankton indicates that the cycle here is also unstable. However, the existence of two generations of most phytophages and their rapid development (thanks to the warmer temperatures) should decrease the period of underutilization of primary production and result in a greater degree of balance between the first two trophic levels. These ideas are confirmed by data on the distribution of bottom sediment in the Southern Ocean.

The zone of rich diatomaceous ooze, indicating underutilization of algae in the pelagic food chains, is bounded on the north by the Antarctic Convergence and interrupted in the western portion of the Atlantic sector, in the region of abundance of *Euphausia superba* (Watkins, 1973).

Thus, the main specifics of the communities of the Southern Ocean can be characterized by: low species diversity; relatively simple trophic web; orderly sequencing of the spatial structure, which changes regularly with time; a long lag between the maxima of phytoplankton and zooplankton and local differences in the degree of their balance.

5. Communities of the Tropical Areas of the Ocean.

(A. K. Heinrich)

The tropical community of the world ocean occupies a tremendous water area, approximately between 40°N and 40°S. Very significant faunistic changes occur at its boundaries--transition to the Arcto-boreal community in the north and the Antarctic community in the south. Many tropical species extend between these parallels throughout all three oceans, and some of them are always among the most abundant species. This creates a structural unity throughout the entire tropical community. However, it is hierarchical in composition and is divided into communities in the individual oceans, which in turn are divided into central, equatorial, distant neritic and neritic. Within these, there are other units of lower rank. Transient communities are found between all of them. The central, equatorial, distant neritic and neritic communities differ from each other most strongly. Our task is a description of the structural and functional peculiarities of the first three types of communities; neritic communities will be analyzed only for comparison.

The biotopes of the central and equatorial communities are the most stable parts of the gyres transferring the primary water masses (central and equatorial), while the biotopes of the distant neritic communities are associated with less stable gyres of the secondary water masses, arising as a result of mixing of the primary water masses (C. W. Beklemishev, 1969). The most extensive and unique distant neritic communities are located in the eastern parts of the oceans, where the eastern equatorial communities and communities of the eastern boundary currents (California, Peru, Canary, Benguela) are found, in the locations of upwelling deep waters. The communities of the currents along the western coasts are influenced by the influx of water from the temperate latitudes. The bases of habitats of certain species are maintained by differently directed currents of surface and deeper layers of water (Longhurst, 1967; Heinrich, 1974b). The biotopes of the neritic communities are located in the smaller circulations near the coastlines. The environment here is much less stable than in the oceanic zones, since it falls under the influence of the variable wind regimes of the coastal upwellings of water and the continental runoff. The boundary, transitional biotopes arise as a result of mixing of waters and have no closed circulation. The position of these communities, according to C. W. Beklemishev (1969), are shown in Fig. 21. The gyres of water maintain the stability of the physical characteristics and allow the species inhabiting them to remain in these regions and pass continually through their life cycles.

The peculiarities of the biotopes and related populations are created by the climate. The peculiarities of the various water masses

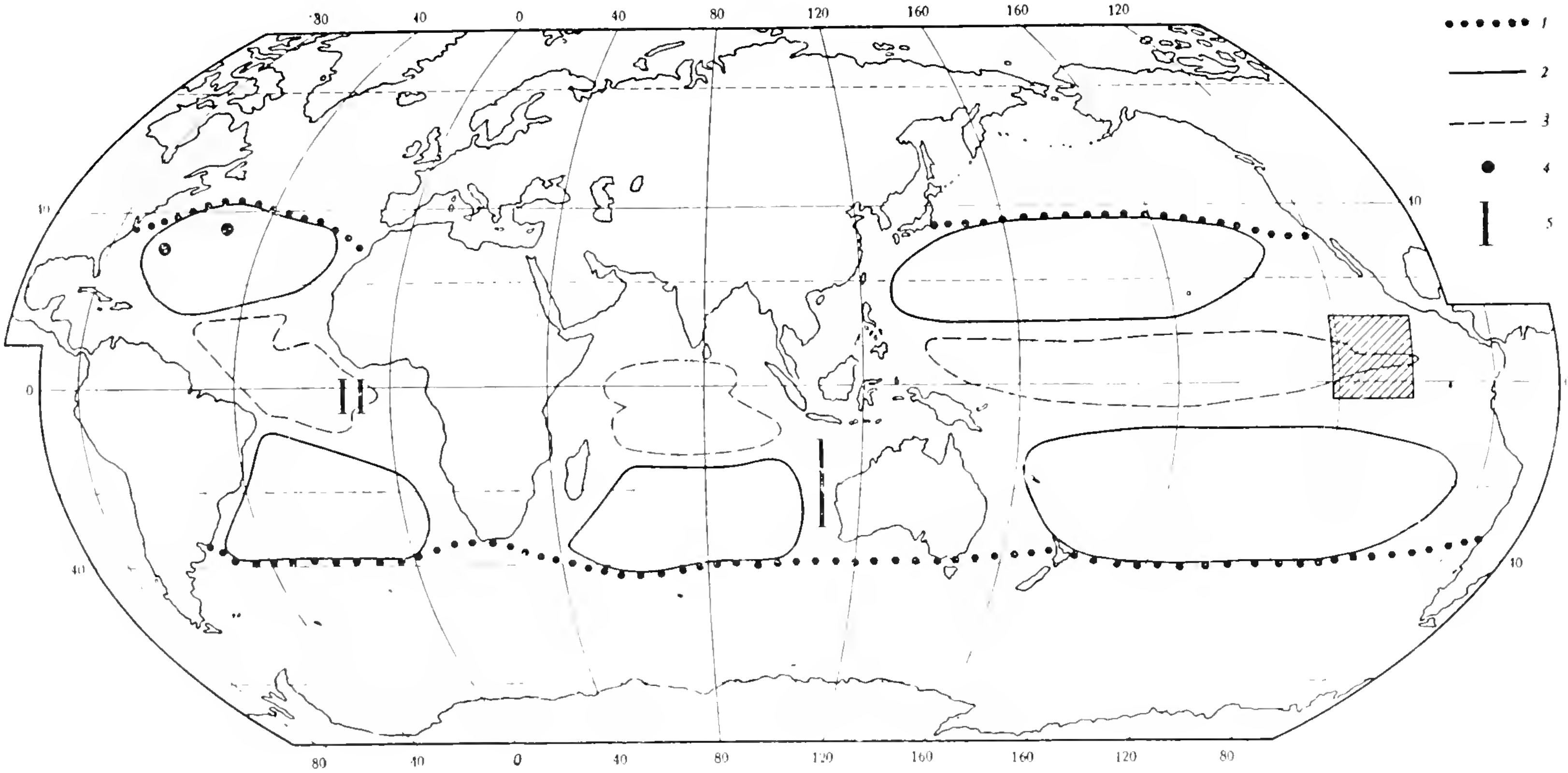


Fig. 21. Position of communities and regions of seasonal observations in the open ocean. Boundaries of communities (after Beklemishev, 1969): 1, Tropical; 2, Central; 3, Equatorial. To the east and west of 2 and 3 we find the distant neritic communities. The stations (4), sections (5), and the shaded region mark the locations of year-round seasonal observations.

forming the biotopes are related to the physical conditions in which they were formed. Therefore, these biotopes are distinguished by the thermohaline characteristics of the waters, the vertical distribution of water density, the predominant directions of vertical water movement, the transparency of the water, the annual mixing cycles, the quantity and composition of nutrients and many other properties which influence productivity and--directly or indirectly--the composition of the population (C. W. Beklemishev, 1969; Bogorov et al., 1968; Koblentz-Mishke et al., 1970: Semina, 1974).

5.1 Structure of Tropical Communities

Peculiarities of species composition and boundaries between communities. Significance of expatriated species. The tropical oceanic communities include a significant number of widespread species. In the oceanic communities of the Pacific Ocean, among the euphausiids, chaetognaths and foraminifers, taken together, widespread tropical species amount to some 60% of the total number (Heinrich, 1975a). In all communities there are also groups of more narrowly distributed species, which have bases of habitats in one or two large-scale gyres only. These are specific species for the communities. Within the communities of the central waters, these include the central (southern, northern and bicentral) species, in the equatorial communities--equatorial species, in the distant neritic communities--transient, peripheral and distant neritic species (C. W. Beklemishev, 1969). Among the euphausiids, chaetognaths and foraminifers, these species represent 19% of those found in the north central community of the Pacific Ocean, 16% of those found in the equatorial community.

Specific species may be absent around the edge of a gyre, so that all species are encountered only in a certain portion of the area. As a result of this, some heterogeneity develops in the composition of the population, even within a single gyre. Furthermore, organisms are transferred from one gyre to another with turbulence and individual streams of water. Turbulent mixing allows plankton to be carried even against the constant current (C. W. Beklemishev, 1969). Many species have broad areas of expatriation. The areas of expatriation of species with various types of ranges cover significant portions of the central and equatorial communities. Due to this, when communities are crossed in the meridional direction, the appearance of certain species and disappearance of others is a normal phenomenon, and the boundaries of the community are not clearly defined (Heinrich, 1975a, b).

Nevertheless, as the use of methods of numerical taxonomy has shown, the differences between the communities are quite genuine, and the zones with the most homogeneous population are generally located within the boundaries shown in Fig. 21 (Heinrich, 1977).

The expatriated species create dependent lower-rank communities within the equatorial and central communities. Their existence results from the influx of water from neighboring communities. Into the equatorial communities central species penetrate from both central communities and the distant neritic species, while into the central communities penetrate equatorial species, peripheral, transient and distant neritic species. The expatriated species have considerable significance in the structure of the communities. In terms of the number of species as a whole for the euphausiids, chaetognaths and foraminifers, in the north central community of the Pacific Ocean, their number is about as great as the number of specific species, and in the equatorial community, they are even 50% more numerous. This indicates the interdependence of neighbouring tropical communities (Heinrich, 1975a).

In tropical ocean communities, the greatest numbers are, as a rule, achieved by the wide-spread tropical species and specific species. Expatriated species are not numerous.

Changes in the number of widespread species. Some questions arise: Just what is the large-scale pattern of distribution of the number of widespread tropical species? Is it similar in different species? Is there similarity between the distribution of areas of abundance of widespread tropical species and ranges of species with relatively narrower areas of distribution, equatorial, central, and distant neritic species? What are the small-scale changes in populations of wide-spread tropical species, and what factors cause them?

Work in the Pacific and Indian Oceans on the distribution of the chaetognaths, euphausiids, copepods, Siphonofora, mollusks (Bieri, 1959; Brinton, 1962; Heinrich, 1960, 1968; Vinogradov, Voronina, 1962, 1963; Chiba, Hirakawa, 1972; Musaeva, 1973; Guérédrat, 1974; Sakthivel, 1973) have shown that the abundance of the widespread tropical species changes significantly from one region to another, and that their distribution is different. If we analyze the large-scale patterns of distribution of population, we can distinguish four main types of distribution: 1) maximum abundance in equatorial waters; 2) maximum abundance in central waters; 3) difference between abundance in equatorial and central regions slight or zero; 4) maximum abundance in one of the distant neritic regions.

Each type has variants, and there are transitions between types. Each type of distribution includes species of all trophic levels. The basic large-scale regularities of horizontal distribution of abundance of animals are retained throughout all seasons, and from year to year (Heinrich, 1968, 1973; Chiba, Hirakawa, 1972; Guérédrat, 1974).

The large-scale pattern of distribution of species of various types can be reduced to the statement that areas of great abundance of some widespread tropical species are located approximately within the regions inhabited by most of the central species, of others--where most of the equatorial oceanic or distant neritic species live. In neighboring regions, over great areas the abundance is small, though there are some small, apparently unstable, spots of higher density.

In the western Pacific, areas have been distinguished for copepoda with each type of distribution, in which most of these species have maximal abundance. These areas diverge spatially quite clearly for the species with the maximum abundance in the equatorial and central regions, and the boundaries between them practically coincide with the boundaries of the equatorial biogeographic province of C. W. Beklemishev (Heinrich, 1968). Each boundary of the equatorial province is the midline between two boundaries, one of which separates the 50% core of the equatorial species, the other the corresponding core of the central species (C. W. Beklemishev, 1969). Consequently, the equatorial, central and distant neritic communities, in addition to the specific species which are theirs alone, are also distinguished by the set of species which reach maximum abundance there.

The existence of groups of species with different types of large-scale changes in abundance is directly or indirectly (through biologic interrelationships) related to the peculiarities of the biotopes of the central, equatorial and distant neritic communities. The combination of these peculiarities is determined by the hydrologic and hydrochemical environments and productivity. It is possible that their combined influence is significant (Fager, McGowan, 1963).

The increase in the abundance of certain species around the periphery of the tropical area apparently results from a decrease in competition, since many tropical species disappear here, and the number of some others decreases (Tokioka, 1959; Voronina, 1962; Heinrich, 1964, 1968; C. W. Beklemishev, 1967).

Relatively small-scale changes in the abundance of species occur within individual communities. In the equatorial communities of the Pacific and Indian Oceans, the position of the band of high abundance of various species is related to the position of divergences and convergences. Transport by currents is also important, as a result of which the bands and spots of high abundance of species, developing one after another in time, also diverge in space (Vinogradov, Voronina, 1962, 1963). Within the northern central community in the western Pacific, the distribution of the maximum abundance of wide-spread tropical species of copepoda of the second and third types of distribution has been found to be connected with the areas of greater productivity located around the halistasis. In the center of the halistasis, where the biomass of zooplankton was minimal (less than 3 g/m^2 in the 0-500 m layer), none of these species produced spots of high abundance (Heinrich, 1968).

Number of species and dominance. The tropical oceanic communities are richest in numbers of species. The number of species varies within the tropical communities. In the tropical regions of the Pacific Ocean, the number of species of euphausiids, chaetognaths and foraminifers changes, when we consider the impoverished peripheral regions, by a factor of 2-3, or if we ignore the periphery, by a factor of 1.5-2 (Heinrich, 1974a). In various taxonomic groups of animals, the changes occur differently. The outlines of regions with the greatest number of species recall the outlines of the ranges of planktonic animals, since in each such group, species predominate with certain types of distribution. However, these regions agree rather well with the boundaries of the equatorial, central and distant neritic communities. Thus, for the chaetognaths, the greatest number of species in the distant neritic communities is characteristic. The foraminifer fauna in the Pacific Ocean is richest in the equatorial community, while the greatest number of species of euphausiids is observed in the central community. The Siphonofora in the Atlantic (Margulis, 1972, 1974) and Indian (Musaeva, 1973) Oceans, as well as the salps in the Atlantic Ocean (Kashkina, 1974) have the greatest number of species in the equatorial and distant neritic communities, rather than in the central communities. The increase in the number of species in communities of a certain type is preserved at least for the chaetognaths in all three oceans.

In the transient communities between the high-latitude and tropical communities, the number of species in all groups is low, in spite of the simultaneous presence of species of different origins, a result of the gradual impoverishment of the fauna toward the periphery of the tropical community. Within the tropical community, the faunistically richest areas are also located in the central, equatorial and distant neritic communities, not in the transient zones between them. The transient biotopes are not favorable for many species from the neighboring communities; therefore, the mixing does not produce enrichment of the fauna in these zones. In the neritic regions, the number of species of planktonic animals is less than in the oceanic ones (Heinrich, 1962; Bowman, 1971).

The tropical oceanic plankton is distinguished by a relatively low dominance of individual species. The dominance varies from season to season and from region to region. In the Indian Ocean, the dominance among copepods increases from regions with stable water stratification or with feebly marking water sinking toward regions with upwelling of water, while species diversity of filtering copepods (based on biomass using the formula of Shannon), conversely, decreases (Timonin, 1969, 1972). Thus, in zones of upwelling of water, 75% of the biomass of Calanoida is accounted for by three species, while outside the upwelling zones, the five or six most numerous species make up only 30-40% of the biomass. A similar picture is observed for the chaetognaths and euphausiids. In the equatorial area of the Pacific Ocean, the intensity of upwelling of water decreases from east to west, and the standing stock of plankton decreases, while the species diversity of large copepods and euphausiids simultaneously increases (Guérédrat et al., 1972), and still greater species diversity of euphausiids is observed in the south central community (Roger, 1974).

Thus, in equatorial communities, where upwelling of water is stronger and more frequent, we can expect a greater dominance of individual species than in the central communities.

In the distant neritic communities in currents along the western coasts of the continents, and in neritic communities, dominance of one or two species is quite clear. In the region of the California Current, an increase has been shown in the dominance of the two most numerous species in the direction from the ocean to the shore, and the species diversity of zooplankton decreases to the shore, as evaluated by the Fisher coefficient (Longhurst, 1967).

Taxonomic and trophic groups. In the tropical oceanic communities, in comparison to the Arcto-boreal communities, the relative quantity of

Gymnoplea decreases, while Podoplea, Ostracoda, Tunicata, Polychaeta, Coelenterata and Chaetognatha increase. Thus, due to the greater relative quantity of Polychaeta, Chaetognatha and Coelenterata, the significance of predators increases. Furthermore, there are many more predators among the Gymnoplea (Heinrich, 1961b, 1968; Timonin, 1969, 1973; Bsharah, 1957; Deevey, 1971; Grice, Hart, 1962; Gordeeva, Shmeleva, 1971; Greze, 1971).

In tropical plankton, in contrast to boreal plankton, a single function in the food chain is distributed more evenly among various taxonomic groups. One good example of the composition of tropical plankton is its composition in the western Pacific in the section along 174°W between 30°N and 30°S. The copepods average about half of the biomass of zooplankton, 2/3 of them being Gymnoplea. About 20% of the biomass is accounted for by the Ostracoda, about the same amount by the Chaetognatha, 10% by the Coelenterata and Polychaeta, while the Tunicata account for a small amount.

Changes in the number, size and, therefore, biomass of the various groups are found along the meridian (Heinrich, 1968). The quantities of many animals (Radiolaria, Foraminifera, Coelenterata, Copepoda, Gastropoda, Chaetognatha) more or less regularly increase in the equitorial region, but the Ostracoda, Amphipoda and Salpidae, conversely, are more abundant in the central regions. In the equatorial region, the biomass of Copepoda amounts to 55-75%, in the central regions--35-50% of the total biomass of zooplankton, the relative quantity of Ostracoda increasing from 10% in the equatorial region to approximately 20% in the central regions. The share of the Salpidae in the total biomass increases toward the periphery of the tropical area.

In the Indian Ocean, primarily within the eutrophic equatorial community, the composition of plankton depends on water regime (Timonin, 1969, 1973). In regions with upwelling of water, Gymnoplea account for 70% of the biomass, in regions with stable water stratification--only 40%. The Chaetognatha are relatively scarce (less than 10%) under conditions of upwelling of water, more numerous (12-27%) under stable stratification or with weaker upwelling of the water. The details of the trophic structure also change. In regions of intensive upwelling of water with high biomass of zooplankton and relatively large numbers of Copepoda, filter feeders predominate (over 50% of the total biomass of zooplankton), among these about 90% being coarse filter feeders. Seizing and swallowing predators make up 20-25% of the total. With weak upwelling of water, the filter feeders are fewer (40%), and half of them are fine filter feeders. Seizing and swallowing predators amount to 30-35% of the total. When there is no upwelling of water, with low zooplankton biomass, filter feeders represent still less (20-30%), while the number of seizing and swallowing predators increases to 45%.

Similar results were obtained in the Bay of Guinea in a study of the relationship of trophic groups among Copepoda in various seasons (Samyshev, 1973) and in the Sargasso Sea, where, during a short period of upwelling of water, a sharp peak was observed in the abundance of the coarse filter feeder Eucalanus hyalinus, while throughout the rest of the year, various species of fine filter feeders predominate (Deevey, 1971; Grice, Hart, 1962).

The zonal changes in the composition of the tropical zooplankton are related to these regularities. Although in equatorial communities, areas may be found without upwelling of water, on the whole upwelling predominates in these communities. Therefore, in the Pacific Ocean, within the equatorial region, an increase was observed in comparison with the central regions in the relative quantity of Gymnoplea.

In the Indian Ocean, areas with predominance of filter feeders are also found within the equatorial community. The central regions are characterized by stable water stratification or water sinking, upwelling being rare and weakly expressed. Therefore, within the central community of the Indian Ocean, between 20 and 29°S, A. G. Timonin found small quantities of herbivorous filter feeders and relatively larger quantities of predators in all locations.

In the Pacific Ocean on the equator between 95 and 160°W, a population which did not fit into this system was found (Vinogradov, Semenova, 1975; Flint, 1975). In spite of clear upwelling of water and abundant plankton, the upper 200 m was dominated by predators, which composed about 60% of the biomass. Toward the west, as the upwelling of water weakened and the biomass of plankton decreased, the relationship of the trophic groups remained essentially the same. As yet, no satisfactory explanation for this has been found, but this composition of the population is not typical for the broad oceanic tropical regions.

Around the peripheries of the tropical area, the relative quantities of Tunicata increase, particularly the Salpidae and Pyrosoma (Heinrich, 1964, 1968). These are filter feeders with a broad diet. This regularity is seen in all oceans. An increase in the quantity of Salpidae has also been noted in certain inshore regions in the lower latitudes and in zones of upwelling of water (Yount, 1958; Russell, Colman, 1935; Rao et al., 1973; Gordeeva, Shmeleva, 1971; Gruzov, 1971). There are insufficient data for comparison but, apparently, at least in the open ocean, these swarms are less frequent and not as great as in the peripheral tropical areas.

In the distant neritic communities of the eastern boundary currents the relative quantity of Copepoda is great, clearly dominated by the coarse filter feeders, both herbivores and omnivores, while predators are few. For example, in the Peru Current, according to M. E. Vinogradov and T. N. Semenova (1975), predators represent less than 10% of the biomass. In the Benguela Current, the large herbivorous and omnivorous Copepoda represent 80-95% of the biomass (Andronov, 1971). In the California Current, in a region of upwelling water, predominance of coarse herbivorous filter feeders (Copepoda and Decapoda Pleuroncodes planipes) is also seen. With increasing distance from the coast, toward the central waters, the relative number of predators increases (Longhurst, 1967).

The zooplankton of neritic communities is usually dominated by the Copepoda. These are most frequently small Copepoda, herbivores or omnivores. One significant feature of the trophic structure of many tropical neritic communities, particularly in regions with strong upwelling water, is the presence of common commercial fish, feeding on the phytoplankton (Heinrich, 1970; Rojas de Mendiola, 1969). Off the coast of California, both in the distant neritic and in the neritic region, the most important herbivore is the pelagic stage of the Decapoda Pleuroncodes planipes (Longhurst, 1967). In the oceanic regions, there are no herbivorous fish, and the food chains are long (Heinrich, 1962; Parin, 1968).

5.2 Production Cycles

The production cycles of communities are seen here as the relationship between the seasonal cycles of the phytoplankton and mesozooplankton and, as possibly, the higher trophic levels. Yu. I. Sorokin (see IV.2) assigns an extremely important role to bacteria, although his conclusions are not universally accepted (Steemann Nielsen, 1972; Banse, 1974; Skopintsev, 1972). Due to the lack of year-round observations of bacteria and protozoa in the open ocean, their participation in the production cycle will not be discussed in this book.

Two extreme types of production cycles are theoretically possible: balanced and unbalanced (Cushing, 1959a). In a balanced cycle, throughout the year the daily grazing of live algae is equal to their net production. Regulation is achieved through the relation of production and consumption of algae, the rate of breeding and growth of herbivores and regeneration of nutrients with an extremely short delay period between the beginning of an increase in the quantity of algae and an increase in their consumption. Similar dependencies occur at the higher trophic levels as well, but the regulation of trophic relationships in nekton animals occurs not so much through breeding as through migration. Stability of abiotic conditions helps to maintain this type of cycle. In contrast to this, with an unbalanced production cycle, the production of algae fluctuates widely due to the effect of unstable abiotic conditions. herbivores develop slowly. There is a long delay period, during which grazing increases to match the increased production of algae; in some cases, this occurs only after the algae reach their maximum quantity which is possible given the reserve of nutrients available. The algae are underutilized for a long period of time. Cushing considered that these cycles do not exist in nature in clear form, but that the tropical communities located outside the regions of strong upwelling of water are closest to the balanced cycles, while the cycles of communities in the temperate and polar waters are closest to the unbalanced cycles.

Factors in the seasonal development of plankton. The physical factors which create instability in the production cycles of tropical communities are primarily those which facilitate the seasonal development of phytoplankton.

In the high-latitude edges of central communities, they are close to those in the boreal area. Thus, in the Sargasso Sea (see Fig. 21), the peak of phytoplankton is formed in the spring, soon after stability is established in the water after the winter mixing, caused by cooling and, possibly, by the winds. In the winter, there are small, short, sporadic pulses of phytoplankton, depending on the weather, since, in contrast to boreal waters, the intensity of light in the winter is not so low as to prevent development of algae. In the summer, thermal stratification is established and phytoplankton is scarce. Its production depends on the recycling of nutrients and random mixing of the water during storms (Riley, 1957; Menzel, Ryther, 1960).

Apparently, in other oceans as well around the periphery of the tropical area the winter cooling is of great significance for the mixing of water, enrichment of the surface layers of the water with nutrients and subsequent development of plankton. For example, in the Pacific Ocean in the region of 40-26°N along 155°W, the winter development of phytoplankton is explained by the deepening of the thermocline due to cooling, as a result of which the nutrients reach the euphotic zone, where they are immediately utilized by the phytoplankton, so that the increase in their quantity is almost unnoticeable (McGowan, Williams, 1973).

In the southern Indian Ocean, to the west of Australia (see Fig. 21), in the region of 18-32°S, the decrease in the quantity of phytoplankton at the end of southern hemisphere summer results from thermal stratification. The increase in the quantity of phytoplankton in the winter corresponds to the breakdown of this stratification. The quantity of nutrients changes very little from season to season, which is also apparently related to the immediate consumption of nutrient salts by the algae (Tranter, 1973).

In the lower latitude tropical regions, winter cooling does not occur, thermal stratification is well developed for a long period of time, and the most important factor in the seasonal development of the plankton is the wind. The winds cause mixing of the water or shifting of currents and the related upwelling of water.

In the eastern Indian Ocean (see Fig. 21), between 9 and 18°S, the increase in the quantity of phytoplankton and zooplankton in the winter is related to the upwelling of water in the southern equatorial current caused by the monsoon (Tranter, 1973). This region belongs to a distant neritic community, but even within the equatorial community of the Indian Ocean, the succession of monsoons has a significant influence on the course of development of plankton (Kabanova, 1968).

In the equatorial community of the Pacific Ocean in the region between 120°W and 180°W from 5°S to 10°N, the maximum of seston is noted in April-June in the Equatorial Countercurrent, and in October-December in the South Equatorial Current, which coincides with the reinforcement of the trade winds (King, Hida, 1957). The periodicity of seasonal changes in the quantity of plankton in the distant neritic community of the currents along the western coasts of the continents is related to the upwelling of water as has been shown, e.g., for the region of the California Current. The upwelling of water itself depends on the wind regime (Walsh et al., 1974).

In the neritic regions, the factors in the seasonal development of phytoplankton include everything which facilitates enrichment of the euphotic zone with nutrients (Heinrich, 1961a, b; Sournia, 1969; Khromov, 1973). Nutrients arrive either from the deeper layers of water or from the land. Therefore, the wind regime mixing the water, driving it away and thereby facilitating upwelling of water, and the regime of precipitation, bringing mineral salts from the land, are both important. However, the seasonal changes in phytoplankton are not the same in all the neritic tropical regions. Local peculiarities change the climatic effects so strongly that even in closely located sections, the seasonal cycle of development of phytoplankton may be quite different (Sournia, 1969; Motoda, Marumo, 1963). In particular, this cycle is influenced by the degree of unevenness of the shoreline, the proximity of estuaries, etc. The earlier assumed (Bogorov, 1941) monocyclic development of phytoplankton in the tropical area, with a winter peak, may be characteristic only of the marginal high-latitude regions.

Peculiarities of production cycles in the main types of tropical communities. Rather complete studies of production cycles of oceanic communities, with observations over the course of a year or more, have been conducted in the regions shown in Fig. 21. The section in the Indian Ocean is located in a distant neritic region, but the composition of the zooplankton during the period of the survey was typical for oceanic regions. Apparently, the course of seasonal phenomena in the southern portion of the section is characteristic for the central community, while in the northern portion it is close to that of an equatorial community. The survey in the Pacific Ocean combines equatorial oceanic and distant neritic sections, which probably differ little from each other in their seasonal cycles far from the coast. Unfortunately, materials have been collected and processed in different regions by different methods and, except for the stations in the Sargasso Sea and the section in the Indian Ocean, the intervals between subsequent observations are longer than a month. In the Guinea Bay, the annual cycle of plankton has been composed, based on data for several years, with observations in any given year lasting only two or three months.

The similarity of a production cycle to any given type can be determined directly by comparing the rates of production and consumption over the course of a year, or indirectly, by keeping in mind the amplitudes of fluctuation of biomass of the various trophic levels, the duration of the delay of consumption, the ratio between the biomass of food organisms and the organisms which feed upon them. Both methods yield only approximate descriptions of a cycle.

The production cycles of oceanic tropical communities are more nearly balanced than the others. For example, in the Sargasso Sea, the Indian Ocean (cross section along 110°E) and in the Central Pacific, the quantity of nutrients, phytoplankton and zooplankton is low and stable throughout the year (Steemann Nielsen, 1958; Cushing, 1959a, b; Menzel, Ryther, 1961; Tranter, 1973; King, Hida, 1957; Blackburn et al., 1970).

The ratio of the quantity of phytoplankton to the quantity of zooplankton is low. In the Indian Ocean in the 0-200 m layer with observations made once per 2 months it fluctuated, based on the content of C, between 1.4 and 6 (Tranter, 1973). In Guinea Bay, in the 0-100 m layer, with observations made once per month, the ratio of phytoplankton to zooplankton, based on wet weight, was 0.05-0.5 (Gruzov, 1971). In the North Atlantic and Polar basin, the ratio of wet weights of phytoplankton and zooplankton is 10-100 in the spring, 1-5 in the summer and less than 1 only in the winter (Bogorov, 1938).

All of this indicates the greater degree of utilization of phytoplankton by zooplankton in the tropical community. According to Steemann Nielsen (1958), the seasonal stability of the quantity of algae and significant homogeneity of their distribution in space, characteristic for oligotrophic tropical regions, can be achieved only as a result of grazing by herbivores. If grazing did not limit growth, the fluctuations, as observed in cultures, would be significant, and at the moment of utilization of the reserves of nutrients, the growth of algae would stop completely, which is not observed in oligotrophic regions. Certain experimental observations confirm this phenomenon as well. In the Sargasso Sea, after relatively large particles (presumably consumers) are removed from the water, the quantity of small particles, primarily algae, increases (Sheldon et al., 1973). In the central waters of the North Pacific, primary production in the euphotic layer agrees simultaneously with the rate of arrival of nutrients from the deeper layers and the rate of excretion of zooplankton (Eppley et al., 1973).

A near balanced production cycle is reached in these regions primarily due to the relatively stable abiotic factors. A second important factor is the short delay period of grazing. For most planktonic Copepoda, breeding continues throughout the year (Guérédrat, 1974; Woodmansee, 1958; Farran, 1949), one generation following another, with no clear domination of any given stage of development. Therefore, as the quantity of phytoplankton increases, the quantity of herbivores can increase rapidly by the growth of already existing juvenile and middle stages and by breeding and subsequent development of a new generation. As the quantity of phytoplankton increases, the breeding rate of the Copepoda increases (Prasad, Kartha, 1959). Judging from observations in inshore regions, generations of tropical Copepoda are short when food is abundant. Off the coast of India, a generation of Acartia erythraea develops in a week (Subbaraju, 1967). The development of a generation of Paracalanus crassirostris in culture requires a minimum of 2 weeks (Lawson, Grice, 1973). Under oceanic conditions, we can expect longer generations, particularly after long periods of starvation, but still, year-round breeding and the varied age composition should help to reduce the delay period.

The structure of oceanic communities, characterized by a diverse species composition, the lack of strong dominance of a few species and a complex, branched food net with many trophic levels can also facilitate a stable production cycle.

Significant differences in the interrelationships of phytoplankton and zooplankton can be found between the equatorial and central communities in the Pacific and Indian Oceans. For example, in the equatorial region of the Pacific Ocean (at 174°W), the ratio of the quantity of phytoplankton to zooplankton is higher than in the central regions. In the equatorial region there is a significant and high correlation between the biomass of phytoplankton in the 0-100 m layer and the biomass of zooplankton in the 0-500 m layer ($r = 0.84$; $P = 0.95$), while in the central regions this correlation is low and insignificant ($r = 0.08$; $P < 0.95$)*.

In the Indian Ocean, within the equatorial distant neritic community, significant positive correlation has been noted (Tranter, 1973) between zooplankton and primary production, zooplankton and nutrients, which is explained by the high value of immediate regeneration of nutrients through the excretions of the animals. In the "subtropical zone" of Tranter, corresponding to our central community, a positive correlation was noted only between phytoplankton and primary production, which determined their direct functional relation, in spite of the weak influence of other effects.

It was found that in the equatorial community of the Indian Ocean, the delay in the development of zooplankton and its grazing of phytoplankton was shorter than in the central community. In the equatorial region, there is no significant correlation between the quantity of phytoplankton and zooplankton upon simultaneous observation. When phytoplankton is compared with zooplankton collected at the same station after one or two weeks, the correlation coefficient becomes higher and significant. When phytoplankton is compared with zooplankton collected after 6-8 weeks, the correlation coefficient decreases once again. In the central community, a comparison of simultaneous collections and collections with intervals of 3-4 weeks reveals a correlation coefficient which is either positive, but low and statistically insignificant, or negative, but comparison of samples collected with a delay of 6-8 weeks yields a higher positive, significant correlation between phytoplankton and zooplankton.

The reason for the long delay period in the central community is the less constant enrichment of the surface waters with nutrients, the greater duration of the period of low productivity, during which the herbivores starve, and the greater grazing of herbivores by predatory micronekton, the population of which is supplemented by drift from the north (Tranter, 1973). The long delay retards the remineralization of nutrients and increases the imbalance. The decrease in the rate of development of animals under conditions of starvation has been proven, at least for neritic Copepoda (Woodmansee, 1958; Ummerkutty, 1967).

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*The decimal logarithms of biomass of phytoplankton and zooplankton were used to calculate the correlation coefficient. The biomass of zooplankton was calculated on the basis of the number and individual weight of the animals (Heinrich, 1961a), the biomass of phytoplankton was taken from G. I. Semina).

During the course of the year, the relationships between phytoplankton and zooplankton change. It is impossible to estimate the length of the periods of overutilization and underutilization by the methods now used. The small fluctuations in phytoplankton and its small quantities during the peak period indicate that there is not a long period of underutilization. Overutilization is possible, but since the mean annual balance is obviously not negative, a status near the balanced state is probably predominant.

In the Indian Ocean, the production cycle in the lower levels of the food chain is apparently better balanced in the equatorial community than in the central community. Due to the shorter delay in the equatorial community, brief periods of underutilization of the phytoplankton are more rapidly eliminated. The high correlations of simultaneously studied zooplankton, nutrients and primary production show that the zooplankton plays the primary role in regeneration of the nutrients. In the central community, the delay in grazing of phytoplankton is longer, and there is no close correlation between zooplankton and the regeneration of nutrients.

In both parts of the section, Tranter also found anomalous, hard-to-explain relations between trophic levels which, in his opinion, resulted from mixing of waters of different origins, thus disrupting the balance.

Attempts at direct estimation of the degree of balance of production of phytoplankton and its consumption by zooplankton over the course of an annual cycle were undertaken in the Sargasso Sea (Menzel, Ryther, 1961) and the Guinea Bay (Gruzov, 1971, 1973). In the Sargasso Sea, the daily needs for the metabolism of all zooplankton in the 0-500 m layer was found to be close to the daily primary production throughout the entire period of observation (2.5 years). If we consider the needs for the growth of animals (which was not done), the total consumption of algae would be still higher. In the opinion of the authors, in the Sargasso Sea the cycles of algae production and herbivore grazing are balanced, and practically all of the production of algae is eaten. The comparisons of Menzel and Ryther (1961) were based on approximate calculation; furthermore, it was not taken into consideration that some of the animals are predators. The peaks in the curves did not coincide precisely, there were delays of 2-4 weeks in the zooplankton, and some of the small peaks in primary production were not accompanied by peaks on the curve of zooplankton respiration.

L. N. Gruzov (1971, 1973) determined the daily consumption of zooplankton in Guinea Bay, based on the needs for respiration and growth of the animals. It was found that over most of the year the trophic relationships of algae and herbivores were balanced, with underutilization occurring only immediately after the upwelling of the water in June. The large generations of herbivores then formed restored the balanced state. It was not stable, and was replaced by overutilization, which was replaced, in turn, by balance with low primary production and a small number of herbivores. A large number of assumptions were made in the calculations; therefore, their accuracy is low, and we cannot say how long the state of balance was retained during the year. However, there were doubtless fluctuations, and the directions of the deviations were probably properly estimated. A more precise estimate of the degree of balance is probably impossible at present.

The annual cycles in the relationships of herbivores and predators in the tropical ocean regions are not nearly so well known. The micronekton, including the animals caught by an Isaacs-Kidd trawl, in the equatorial region of the Indian Ocean produce an annual maximum of biomass after the maximum of mesoplankton. The highest correlation coefficient between zooplankton and micronekton, i.e., small fishes and squids, is obtained by comparison of samples collected at intervals of 6-12 weeks (Legand, 1969; Tranter, 1973). This is explained by the longer development of the larger animals. However, in the central region, and in some seasons also in the equatorial region, no such regularity is observed. It is assumed that under these conditions the zooplankton and micronekton are related to the mixing of waters of different origins. The quantity of micronekton in these regions is more stable than the quantity of zooplankton or the value of primary production. Here, advection increases the stability in the interrelationships of the higher levels of the trophic chain (Tranter, 1973).

In the eastern Pacific (see Fig. 21), the amplitude of seasonal fluctuations of fishes and squids is similar to that observed for algae and zooplankton, but the maximum of their biomass occurs during the period of the minimum of zooplankton, meaning that there is a delay of four months when observations are made once each two months. The seasonal changes of biomass of micronektonic crustaceans are statistically significant only at the Equator; their maximum coincides with the maxima of phytoplankton and zooplankton (Blackburn et al., 1970).

Thus, due to the longer period of development of micronekton, its increase in quantity lags behind the increase in quantity of zooplankton by 1.5-3 months, which introduces elements of instability to the balance of production and consumption. Sometimes, the quantities equalize at various times in the year due to advection, while in other cases advection, probably, may lead to the opposite result. The amplitudes of fluctuations of the quantity of micronektonic fishes and squids are not great. In the eastern Pacific, their quantity during the maximum is approximately double that observed during the minimum, and their seasonal variability in both communities of the Indian Ocean is still less (Blackburn et al., 1970; Tranter, 1973). The fluctuations in the quantity of micronektonic crustaceans in the eastern Pacific are quite small, with the exception of the Equator, where the maximum is 15 times greater than the minimum (Blackburn et al., 1970). This has not as yet been explained. As we noted earlier, this region is also distinguished by a unique composition of plankton.

Large nektonic animals (tuna, whales) in the Indian Ocean migrate to the areas of seasonal concentration of micronekton, with which they are connected primarily through the squids and certain fishes, immediately before its maximum (Tranter, 1973). This increases the stability of the trophic relationships.

In many tropical neritic communities, in contrast to the oceanic communities, the trophic relationships of phytoplankton and herbivores are essentially unbalanced (Heinrich, 1970) for long periods of time. The phytoplankton is abundant and underutilized. The fluctuations in quantity of phytoplankton are great. Along the west coast of India, e.g., the number of algae during the maximum exceeds their number during the minimum by a factor of 150 (Subrahmanyan, 1959), and the maximum mean monthly biomass of algae in the Gulf of Panama is 67 times greater than the minimum one (Smayda, 1966). The ratio of the quantity of phytoplankton to the quantity of zooplankton in the Gulf of Panama varies from 0.04 to 980, averaging 83, and at times reaches ratio characteristics for boreal communities (Smayda, 1966). Based on the calculations of this author, the daily rate of grazing of phytoplankton by herbivores is only 20-44% of the daily primary production.

The weak balance of trophic relationships in neritic tropical communities in comparison to oceanic communities is explained first of all by the instability of environmental conditions, the strong but inconstant enrichment with nutrients as a result of upwelling of water and runoff from the land. In places where, as at the Great Barrier Reef, the mixing regime is constant, and there is no runoff from the land, the quantity of phytoplankton is low and its fluctuations are slight throughout the year (S. M. Marshall, 1933). Furthermore, neritic communities have a simpler structure than oceanic communities (smaller number of species, with relatively strong dominance of a few species, predominance of short food chains). This reduces the possibilities of regulation of trophic relationships of the organisms and thereby facilitates instability in the production cycle.

The distant neritic communities in the eastern boundary currents are, like the neighboring neritic communities, under the influence of strong upwelling of variable intensity. Some of the nutrients and phytoplankton may reach there due to advection from neighboring neritic regions. These regions are dominated by large herbivorous Copepoda, while herbivorous fishes are not of essential significance. In the California Current, Pleuroncodes planipes is abundant both in the neritic and in the distant neritic region (Blackburn, 1969). Changes in the intensity of upwelling of water during the course of the year lead to alternation of oligotrophic and eutrophic periods and changes in the trophic relationships in the community (Cushing, 1971). For example, in the Peru Current in September-November, phytoplankton is consumed in the regions off the shelf quite intensively, while in June there is much less zooplankton, and the consumption of phytoplankton has been estimated to be less than 10% of its daily production (Beers et al., 1971; Heinrich, 1974b; Rat'kova, 1975). Significant seasonal changes also occur in the California Current (Walsh et al., 1974).

The greatest changes in trophic relationships should occur when a period of relative stability is replaced by a period of upwelling of water, and vice-versa. Apparently, at the beginning of upwelling of the water one can expect a delay in grazing and underutilization of phytoplankton, particularly since these regions are dominated by relatively large, slowly developing Copepoda. Probably, in these communities the underutilization of phytoplankton is less strongly expressed than in the neighboring neritic communities, but more strongly than in oceanic communities. In the band of great abundance of large herbivorous Copepoda, located along the edge of the shelf in the region of the Peru Current, there is quite intensive grazing of phytoplankton even when in the neighboring neritic region the concentrations of phytoplankton are high, and it is clearly underutilized (Heinrich, 1974b).

6. Deep-Water Communities.

(M. E. Vinogradov)

Communities of the meso-, bathy- and abyssopelagic zones live below the producing surface zone of the ocean and inhabit basically the intermediate, deep and benthic waters.

Energy dependence. Communities inhabiting waters below the euphotic zone have practically no producers of their own. In a few regions, chemosynthesizing bacteria act as producers, but the organic matter which they form plays a clearly subordinate and local role in the overall balance of organic matter in the ocean. Thus, all communities of the meso-, bathy- and abyssopelagic zones are energetically dependent on communities in the producing zone and cannot be looked upon as viable biocenoses in the meaning of Yu. Odum (see I.1).

However, there is a permanent, and at times very intensive exchange of population between the communities of the various vertical zones. For example, the population of interzonal herbivores in the cold-water regions of the ocean feeding in the surface zone, descends to depths of 1000-2000 m. They make up almost half of the mass of the population of the meso- and bathypelagic zones, and are the most important components of both the surface and the deep-water communities. From this standpoint, the surface and dependent deep-water communities can be considered as a part of a single, larger community, encompassing all or almost all of the depths of the oceanic waters, and this mass with its population can be looked upon as a single ecosystem. Nevertheless, the population of the mass of water is stratified, which allows us to speak of communities characteristic for various depths, and to study their specific features.

Energy enters the communities of the ocean depths with organic matter formed in the surface layers, in the euphotic zone. By whatever path this matter reaches the depths of the ocean, in the form of products of metabolism of the animals living in the higher levels or in the form of their dead remains, in the bodies of animals performing vertical migrations, carried down from the coast and shelf by benthic currents, in any case the quantity of this organic matter decreases as it descends into the deeper layers due to consumption by the population of the intermediate depths and mineralization. Therefore, as depths increase, the population of the pelagic zone finds itself living in conditions of ever-increasing food shortage. The concentration of plankton decreases with depth roughly exponentially.

In those regions of the ocean where the productivity of the plankton of the euphotic zone is higher, the quantity of deep-water plankton is also higher, and the change in the structure of its communities with depth is slower than in oligotrophic regions.

The quantity of deep-water plankton may be influenced not only by the production in the euphotic zone, but also by the balance of life cycles of the surface communities, which determines the degree of utilization of this production within the communities of the euphotic zone itself (Banse, 1964). The lack of experimental determinations of the ecologic and physiologic characteristics of deep-water plankton prevents us as yet from testing this statement. If the structure of the deep-water communities differs beneath water areas with differing balanced cycles of surface plankton, this dependence may not arise at all (Vinogradov, 1968).

At the very least, in the temperate and cold water regions of the ocean the flux of organic matter from the surface layers into the depths undergoes seasonal cyclic variations. The seasonal unevenness of delivery of food, obviously, must cause seasonal variation in the life cycles of deep water fauna. Actually, even at ultra-abyssal depths (below 6000 m) in the waters of the Kuril-Kamchatka trench, seasonal variations in the age population structure of certain pelagic animals have been detected (Vinogradov, 1970a).

We should not forget that as depths increase, not only the quantity of food, but also its nature, changes. As a result, the type of nutrition of the main mass of plankton changes, and there is a change in the dominant trophic groups with depth. All of this significantly influences the species and spatial structure of deep-water communities.

Tendency to decrease energy expenditures. In the highly productive boreal regions of the Pacific Ocean, phytoplankton fixes approximately 110 g of carbon for each square meter of surface each year, while in the oligotrophic central waters of the tropical zone, carbon fixation is only 28 g, i.e., some 4400 and 1100 g of wet organic matter is produced beneath each square meter each year (Koblents-Mishke, 1965). If we know the distribution of biomass of zooplankton in the world ocean and assume that its production in the subpolar waters is 1.5 times greater (Yashnov, 1939), and in the tropical waters is 7 times greater (Steemann Nielsen, Jensen, 1957) than the maximum biomass, we can calculate that for the upper 200 meter layer in both regions the ratio of primary production to production of zooplankton (P_p/P_z) is approximately 45-50, i.e., 1 gram of production of zooplankton requires 45-50 g of production as wet organic matter in the phytoplankton. Riley (1951) believes that only 10% of the organic matter produced in the surface zone ever gets below the 200 m level. Considering this information and assuming that the annual production of the deep-water plankton is approximately equal to the biomass or somewhat less, it is easy to see that at depths of 200-1000 m, the ratio of P_p/P_z in the subpolar regions is 3-5*, in the tropics--ignoring

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*The biomass of plankton in the 200-1000 m layer includes the upper interzonal species. Excluding these, the P_p/P_z ratio will be approximately doubled.

macroplankton--20, considering macroplankton, approximately 8-10. In other words, animals living at lower than 200-1000 m receive approximately 5-10 times less energy per unit of biomass than animals in the surface layers. If we compare the energy balance of the surface animals and the animals living below 1000 m, the difference will be still greater.

It should be kept in mind that interzonal migrating species feeding in the surface layers represent a significant fraction of the plankton only down to depths of 500-1000 m. At greater depths, particularly in the tropical regions, their significance decreases rapidly and the unique food relationships of the oligotrophic bathypelagic zone are clearly seen.

In the food-rich surface layers, even significant energy losses, related to the active movement of the animals, can be comparatively easily compensated for by increasing the intensity of feeding. In the poorer deep waters, this is not always possible. It is believed (Jørgensen, 1966) that the energy expenditures of plankton filter feeders are expedient only if the quantity of organic detritus which can be assimilated from the water is over 25 mg/liter. Actually, the quantity of organic detritus in the deep waters is 0-32 mg/liter as protein equivalent, or 0-70 mg/liter as organic matter.

Adaptation to existence under conditions of extremely scarce food resources in groups having different types of nutrition may be manifested differently and to a different extent. However, the tendency to reduce the expenditure of energy is inherent in the entire population of the depths. The upper and interzonal animals, which spend only a part of their life cycle in the deep waters, decrease their metabolic level sharply at this time. For example, Calanus hyperboreus, which descends in the winter to a depth of 500-2000 m, decreases its energy expenditure for respiration by a factor of 3. This change in the intensity of respiration is purely adaptive and is independent of temperature. Calanus, remaining in the deeper layers for the winter, is in a unique state of anabiosis (Conover, 1962).

As the depth increases and the food resources decrease, the mean dimensions of animals change. They increase significantly for predators and certain other forms in the bathypelagic zone. In the abyssopelagic zone, the role of predators, as we have stated, is gradually reduced to nothing and, therefore, the mean size of zooplankters decreases (Vinogradov, 1968). The increase in the dimensions of carnivorous forms results not only from predominance of representatives of larger genera of animals, but also from deep-water gigantism. The essence of this phenomenon is an increase in the dimensions of animals of the same genus or similar genera with increasing depth. For example, in various species of the genus Sergestes, the mean dimensions increase from 27 mm (S. vigilax--habitat 110-650 m) to 94 mm (S. robustus--habitat 550-800 mm); for Taaningichthys, the corresponding figures are from 65 mm (T. minimus--mean depth of habitation 475 m) to 95 mm (T. paurolychnus--mean depth 900 m); for euphausiids of the genus Stylocheiron--from 6 mm (S. suhmi--mean depth 25 m) to 30 mm (S. maximum--mean depth 550 m). Attempts have been made to explain this phenomenon by the effects of various abiotic factors, primarily pressure and temperature

(Wolff, 1956; Birshtein, 1963; Belyaev, 1966). However, V. B. Tseytlin (1975) has shown that the primary factor determining the increase in dimensions of zoophagous forms with depth is the decrease in the quantity of food resources available. The drop in temperature also plays some role. Based on food consumption and its variation with temperature, V. B. Tseytlin has developed a method for estimating changes in the dimensions of similar species of carnivorous animals with increasing depth and decreasing food concentration and temperature. The results produced correspond well to those observed in nature.

In nonpredatory groups, changes in dimensions are more difficult to follow, but it has been noted that in the abyssopelagic zone, smaller forms predominate than in the higher layers. This is probably related to the fact that the fine filter feeders, which satisfy their demands with smaller quantities of foods, have an advantage there. The decrease in the mean dimensions of filter feeders does not result from a decrease in the size of species in the genus--their dimensions may even increase, as in the case of the predators--but rather due to predominance of genera with smaller species.

The principle of economy of energy expenditures leads to radical restructuring of the entire organism (Denton, Marshall, 1958; N. B. Marshall, 1960; Walters, 1961; Vinogradov, 1968; etc.). The basic adaptations move in the direction of creation of neutral buoyancy, so that the animal can remain in the suspended state without expending muscular effort, thereby decreasing the rate of active metabolism.

The comparatively good food supply for fishes found in the surface zone allows them to lead an active mode of life. Preservation of buoyancy, which is near neutral, with extreme changes in depth of habitation (and, consequently, hydrostatic pressure) and temperature of the environment is possible only by active, rapid changes in the volume of the swim bladder. This requires well developed musculature, a strong skeleton for the attachment of this musculature and a system for rapid liberation of oxygen from the blood into the swim bladder and for its rapid absorption by the blood. All of this requires significant energy expenditures. Active hunting is possible only with high mobility, while developed sense organs (particularly vision), a complex brain structure, strong musculature, and, consequently, intensive metabolism. All of this draws a basic distinction between the nekton inhabiting the rich epipelagic and mesopelagic layers from the true deep-water residents.

In fish which do not rise into the surface zone and live at depths of over 500-1000 m, as well as most of the deep-water pelagic invertebrates, neutral buoyancy is achieved by means not requiring additional expenditures of energy. A decrease in specific weight is achieved primarily by reduction of the content of heavy tissues. The bony skeleton is replaced by a cartilaginous skeleton, and muscle fibers are weakened. The subcutaneous layers and spaces between muscle fiber bundles are filled with gelatinous mesenchyma, and a portion of the subcutaneous cavities--with fat. Most of the soft tissues are gelatinous in consistency, as a result of which the mean content of water in the tissues of deep-water fishes is 2.5 times higher than that of shallow-water species (Walters, 1961). The swim bladder loses its main purpose, that of maintaining neutral buoyancy with changing pressure, and either disappears completely or is reduced and filled with fat. The tissues of the bladderless bathypelagic fishes are 2-4 times poorer in protein than those of the shallow-water species (Denton, Marshall, 1958). The decrease in basic metabolism also results from a reduction in the sensory organs.

The reduction in musculature leads to simplification of the circulatory and excretory systems. In deep-water pelagic fishes, the surface of the gill leaflets is greatly reduced, decreasing the respiration rate. The low rate of respiration and secondarily simplified excretory system indicate a low level of metabolism and a corresponding decrease in energy expenditure. And, in fact, measurements of the metabolic rate of certain deep-water fishes at the depth where they live have shown that it is two orders of magnitude lower than that of shallow-water fishes of the same size (Smith, Hessler, 1974).

The weak development of musculature and the systems of organs which serve it and the low rate of metabolism are possible only with extremely limited mobility of the animals. Deep-water animals are almost all predaceous, but cannot be predators which actively seek out and chase their prey, but rather only passively attracting predators. This has been confirmed by direct observations. For example, J.-M. Peres, observing the behavior of Chauliodus sloanei from the bathyscaphe, writes, "These fish float motionless in the water, the longitudinal axis of the body inclined at an acute angle to the horizontal, so that the head is higher than the tail. The long second ray of the dorsal fin, equipped with a luminous organ, is extended forward above the head, so that the tip of the ray is in front of the mouth." Cyclothone and Gonostoma are "always immobile, floating passively; they wait for their prey, rather than following it; I saw no motion of the fins, with which they maintain their equilibrium" (cited by Marshall, 1960, p. 110, 107).

In many deep-water Decapoda, the carapax are much thinner than in the animals living higher up; let us compare, for example, Hymenodora frontalis, with its comparatively hard external skeletons, and the deeper-water species H. glacialis, the external skeleton of which is quite fragile, or the strong Systellaspis and Oplophorus with the very fragile Notostomus, etc. In the deep-water cephalopod mollusks (Vampyroteuthis, Vitreledonella, Amphitretus, Japetella, Eledonella, etc.) have lost most of their supporting and muscular tissue. A thick layer of jelly-like subcuticular tissue has developed, while the muscles have partially degenerated and are also replaced by jelly-like tissue, so that the consistency of these cephalopods is similar to that of medusae. Thus, even the large inhabitants of the depths are passive planktonic animals, not active nektonic animals.

Passive waiting, rather than active hunting, for food is characteristic of deep-water invertebrates as for deep-water fishes. This is indicated, in particular, by the (sometimes greatly) elongated extremities, allowing testing and feeding in a large volume of water by cephalopods and crustaceans, and the weak development of the eyes of deep-water decapods and mysids. For example, Chiroteuthis and Mastigoteuthis have greatly elongated tentacles, which may be 5 or 10 times as long as the body. The anterior appendages of certain predaceous deep-water Copepoda are greatly enlarged by lengthening of the segments of the basipodite of the second maxillipeds and have sparse but long, strong setae. In a living specimen (Wickstead, 1962), the feeding appendages are extended downward and forward and form a trap which snaps shut whenever prey enters it. However, the predaceous copepods do not attempt to follow prey which floats past.

Thus, the adaptations related to the peculiarities of existence and attempts to reduce the expenditure of energy are quite radical and varied. They change the appearance of pelagic deep-water animals much more than do adaptations to changes in other factors of the environment. In other words, changes in the food supply, not changes in physical parameters such as light, pressure or temperature, are most important in determining the peculiarities of morphology of the pelagic animals at different depths.

The principle of economy of energy expenditure is apparently not limited to a decrease in the level of basic and active metabolism. In the opinion of V. Walters (1961), one important path of evolution in waters poor in food resources, such as at great depths, is neoteny. Neotenic development eliminates the catabolic phases of the life cycle and the morphogenesis of "mature" structures. As a result, the animals need less energy for the attainment of sexual maturity.

Peculiarities of the breeding of deep-water animals are also related to the acquisition of food. Two paths of development of juveniles are possible for inhabitants of the food-poor deep waters: either production of a large number of small eggs, with the small, weak larvae feeding in the food-rich surface zone, or the production of a small number of large eggs, rich in vitellus, so that the embryos can pass through a number of metamorphic stages before hatching. The large, lecithotrophic larvae, when they first hatch, need not (or almost need not) feed, if there is no suitable food available, and later are capable of utilizing large, scattered food objects, which could not be eaten by planktotrophic larvae. The former path is characteristic for most deep-water pelagic fish. The latter has been followed by only a few, primarily benthic, deep-water species (certain Apoda, some of the Macruridae, Liparidae, etc.), although this path is followed by the overwhelming majority of deep-water higher crustaceans (Decapoda, Amphipoda, Euphausiacea, Mysidacea, etc.) and many Cephalopoda.

The direction of evolution is also related to a great extent to the food resources: Where food is abundant, highly fertile species are primarily produced, with short life cycles and a broad range of adaptation, while under conditions of limited food supply, relatively less fertile, narrowly specialized species with long life cycles are found (Shmal'gauzen, 1968). The abundance of food resources also defines the structure of the pelagic communities at various depths.

Considering the above facts and data on the variations in quantity, specific composition and predominance of various trophic groups (II.1) with depth, we can attempt to provide a brief description of the structure of the communities of the meso-, bathy- and abyssopelagic zones.

Mesopelagic zone (200-750÷1000 m). Most of the population consists of species directly related to the surface zone and feeding in it during their ontogenetic or diurnal migrations. The concentration of zooplankton here, in some cases, particularly in temperate and cold-water regions, is almost as great as the concentration in the surface layers. In addition to the migrating animals, bacteriophages are also important (Radiolaria, Phaeodaria, etc.), utilizing the high concentration of bacteria and single-celled heterotrophs, usually found at depths of 500-700 m (Sorokin, 1971a). In addition to migrants (carnivores and herbivores), predatory forms which do not migrate to the surface layers are also significant (see II.1). The communities are highly varied, almost equal in species to communities of the surface zone in the tropics and more varied than communities in the cold-water regions.

Bathypelagic zone (750÷1000-3000 m). Communities are characterized by comparatively low population and biomass, no greater than 20-30 mg/m^3, even in the most productive regions of the ocean, with significant predominance of carnivores over detritophages and herbivores, among which, in the cold-water regions, the upper-interzonal filter feeders are still important. In the upper levels of the bathypelagic zone, they may make up as much as 30-40% of the mesoplanktonic biomass.

The main mass of the population consists of predatory forms, utilizing the organic material which enters this zone from the surface zone. However, most of the predators are passive--they do not chase their prey, but rather attract it. The sparsity of the food resources and the need to reduce the expenditures for active and basic metabolism lead, in many groups, to significant morphologic restructuring. As a result, the fauna differs taxonomically from the surface fauna. This is particularly true of groups present in the surface layers as active predators, in the bathypelagic zone as species which have gone over to passive waiting for food (Birshtein, Vinogradov, 1971).

The variety of the community is great; many groups of pelagic animals reach high species diversity here. The lower population, with comparatively larger number of species, means that the dispersion of the distribution of individual species is significantly greater than at lesser depths. The increase in the diversity index of communities indicates an increase in stability, which, according to Margalef (1963b), allows the community to continue its existence with a smaller quantity of energy entering the system, i.e., with more limited food resources.

Abyssopelagic zone. Communities inhabiting depths over 3000 m have been very little studied. The biomass and number of plankton are extremely low, and decrease with depth. No group has its maximum species abundance below 3000 m. In contrast to the bathypelagic community, the abyssopelagic community might be called oligomictic. The extreme sparsity of plankton, apparently, makes even passive predation energetically inexpedient, and carnivorous species almost disappear. The plankton at these depths consist primarily of small detritophages or omnivores. The species poverty of the abyssopelagic zone results also from the fact that, given the great sparsity of the population, the dispersion of the distribution of individual species increases so greatly that the sexes do not encounter each other sufficiently frequently to breed. The population of the greatest depths, having the lowest total number, can exist only with comparatively homogeneous species composition.

CHAPTER III. BENTHIC COMMUNITIES AND THEIR STRUCTURAL AND FUNCTIONAL CHARACTERISTICS

1. Littoral Communities. (O. G. Kussakin)

The boundary of the ocean is generally considered to be the line of zero depth, representing the lowest possible tide for a given area resulting from purely astronomic causes. However, the influence of the ocean is very strongly felt along the shore at points located slightly higher than the zero depth line. Therefore, the intertidal zone and supralittoral areas, although they are located above the zero level, i.e., formally belong to the land, are considered zones of the sea.

The intertidal zone, or drying zone, is defined as the zone located between the high and low tide marks. Thus, its lower boundary is the zero depth level, and its upper boundary is the highest theoretically possible tidal level. Consequently, the intertidal zone is a zone which is periodically flooded with water, and periodically exposed, subjected to the action of the air. The amphibiotic nature is its most characteristic feature. Although its vertical extent is extremely small (from a few centimeters to 16 m in the Bay of Fundy), if the shoreline has a gentle slope the width of the intertidal zone may be as much as several kilometers. No matter what the width of the intertidal zone, the degree to which it is amphibiotic changes a great deal from its top to its bottom; therefore, the conditions for the life of littoral organisms change a great deal over a small distance. In spite of the fact that the intertidal zone is a zone which is transitional between the land and the sea, the overwhelming majority of its population consists of marine plants and animals, although in certain places, particularly those protected from the surf, specialized forms of land organisms predominate--marsh halophytes and mangroves.

Its boundary position between the two main habitats of life--the air and the water--and the amphibiotic conditions present there distinguish the intertidal zone among all other zones of the sea. The daily and seasonal fluctuations in temperature, salinity, moisture content, etc., are most sharply reflected here. Great expanses of the coastline in the Antarctic, Arctic and temperate latitudes are covered in winter with ice which, on the one hand, has a destructive, abrasive influence, but on the other hand, protects the inhabitants of the intertidal zone from the effects of the extremely low air temperatures.

Above the intertidal zone is the supralittoral zone, which is also subject to the influence of the ocean, though to a lesser extent. This zone is flooded with water only sporadically, during strong onshore winds or severe storms. The rest of the time, the supralittoral is irregularly wetted by spray from the surf, and in friable soils, by capillary rise of sea water. In this area, the forms of terrestrial origin predominate as to number of species (insects, arachnids, flowering plants, etc.), although in the quantitative aspect, specialized forms of marine origin may dominate (Talitridae Amphipoda, in the tropics--crabs, etc.).

1.1 Zonality of the Intertidal Zone

The question of the principles of vertical subdivision of the intertidal zone into systems of coordinated units of lower rank has been discussed approximately since the middle of the last century. The expediency of this type of subdivision is beyond doubt, since the vertical stratification of organisms and their complexes is particularly clearly manifested in the intertidal zone, and frequently, particularly if the shoreline is not broken, groups of flora and fauna (communities) may extend almost without interruption for hundreds of kilometers, forming clear stripes but a few decimeters or even centimeters in width. However, the question of the principles upon which the subdivision of the intertidal zone should be based remains in dispute.

It would seem most simple to accept the biotic principle, i.e., to divide the intertidal zone in accordance with the communities or types of communities--formations forming the strips along the shoreline, which we observe in nature, particularly since they are not distinguished by great variety. The overwhelming majority of schemes of this type, however, have reflected the specifics of only a limited sector of the shoreline and are therefore only of historic interest. The greatest of the schemes of this type is the universal scheme of zonality suggested by T. A. and E. Stephenson (Stephenson, Stephenson, 1949) for a rocky intertidal zone. The Stephensons subdivide the intertidal zone into three "zones," each with its own typical inhabitants, usually relating to the same life forms, but with different species or genera in the different regions: the supralittoral edge, or the littorine zone; the middle littoral zone or the barnacle zone; the sublittoral, or infralittoral edge. Later, an attempt was made (Dahl, 1953) to provide a similar system for an intertidal zone with friable sediment. One significant shortcoming of such a system, like others based only on the distribution of organisms, is the failure to give proper weight to the significance of tidal variations in sea level as the primary factor defining the vertical distribution of the organisms and their communities in the intertidal zone. Furthermore, harder sediments, sand and mud do not have common communities; therefore, the systems developed for different sediments are different and difficult to compare and, finally, the leading groups of any sediment, if they are cosmopolitan, may be located at quite different levels, due to differences in temperature and salinity of the water, insolation, surf power, etc. Furthermore, even under similar conditions, the vertical distribution of indicator species is not always constant. For example, in the British Isles, the upper boundary of the middle intertidal zone, defined according to the upper boundary of massive accumulation of barnacles, is significantly higher where Chthamalus stellatus predominates than where Balanus balanoides, which lives at a lower level, dominates. Thus, systems based on indicator organisms and their communities cannot yield universal vertical boundaries for subdivision of the intertidal zone.

Of the abiotic factors acting on the composition and distribution of littoral communities, the most important, essentially determining the specifics of the intertidal zone as an independent zone, are the tidal fluctuations in sea level. The relationships between the durations of periods of immersion and exposure to air in different parts of the intertidal zone determines, basically, the vertical stratification of organisms and their communities in this zone, which is manifested quite clearly in all climatic zones. The principle of relating the vertical boundaries within the intertidal zone to the levels of the neap and spring tides, as well as the mean sea level for European shores with true semidiurnal tides, was first clearly formulated by L. Vaillant (1891), then later successfully used by a number of researchers (Pruvot, 1897; Beauchamp, 1914; Gurjanova et al., 1925. 1930a, b). According to this principle, the intertidal zone is subdivided into three horizons, of which horizon II, or the middle horizon, is bounded by the mean low water stages and mean high water stages, while horizon I, the upper horizon, and horizon III, the lower horizons are determined by the boundaries of the littoral itself. Each horizon is divided into two stages, the boundaries of the stages being the mean high water and the mean low water springs for the upper and lower horizons, while the middle horizon is divided by mean sea horizon. The use of the principle of Vaillant, developed for an intertidal zone with true semidiurnal tides, is quite difficult in those coastal areas where other types of tides occur. P. V. Ushakov (1951) has shown that the principle of Vaillant is applicable to conditions of irregular semidiurnal tides, but the boundaries of the stages are defined differently: In horizons I and III, these boundaries are the mean high water and mean low water springs. We consider that the principle of Vaillant can also be applied to intertidal zones with diurnal and irregular diurnal tides, although in these cases it is not the levels of the springs and neaps which are characteristic, but rather the levels of the tropical and equinoctial tides (Kussakhin, 1958a, 1961). It is interesting in any case to subdivide the middle horizon into two stages with a boundary at mean sea level.

With this expansion of the principle of Vaillant in all cases the upper horizone of the intertidal zone remains above water most of the time, exposed to the air for several days in a row (during the equinoctial or neap tides). Conversely, the lower horizon spends most of its time beneath the water, and is exposed only during the lowest (spring or tropical tides; the middle horizon, with all types of tides, is characterized by periodic daily immersion and drying out. Similar conditions will be observed in corresponding stages with all types of tides.

In addition to the tidal fluctuations in sea level, the vertical stratification is greatly influenced by the force and constancy of the surf. An increase in strength of the surf usually results in shifting of the littoral communities upward. Sometimes, this displacement may be as great as several meters vertically; in these cases, the entire intertidal zone may be occupied by purely sublittoral communities, with the true littoral community shifted far upward. Of the biotic factors, competitive relationships may greatly influence the vertical distribution of organisms. In many cases, there may also be seasonal changes in stratification of communities, with this type of displacement observed in all climatic zones.

Schemes like the scheme of the Stephensons, which combine the characteristic features of vertical stratification of the basic communities, can be used only in comparative ecologic studies, always in combination with subdivision of the intertidal zone according to the principles of Vaillant.

Of course, when used in this manner, the terminology of the Stephensons must be slightly altered, since the "zones" of the Stephensons--the supralittoral edge, the middle littoral zone and the sublittoral edge--are not considered by us to be the primary subdivisions of the intertidal zone, but only characteristic types of formations of rocky facies of the intertidal zone. We consider it expedient to call them systems or divisions. Since the term "middle littoral zone" might be easily confused with the middle, or second, horizon in the system of Vaillant, we propose to apply the term "true intertidal zone" or "true littoral division" (eulittoral) to this division.

In nontidal seas, like the Black Sea and Baltic Sea, where there is no true (tidal) intertidal zone, there are communities quite similar to littoral communities, though their vertical stratification is much less fully developed. In these seas, there is a special zone, which has come to be called the pseudolittoral, which owes its existence to the surf waves (Mokiyevskiy, 1949). O. B. Mokiyevskiy accepts the upper edge of the maximum surf spread as its upper boundary, the lower edge of the beach, where the surf wave is obstructed, as its lower boundary.

1.2 Factors Specific for the Littoral

The nature of the connection between the sea coast and the ocean or open sea has a great influence both on the abiotic conditions of the littoral environment, and on its population. Open, unprotected shores are usually subject to strong surf action, the surf becoming weaker with increasing distance from the ocean, and practically disappearing in partially closed bays and lagoons. The role of the surf in the conditions of the intertidal zone is very significant and quite varied. First of all the surf, wetting the intertidal zone partially neutralizes the effect of the tidal factor, particularly at low tide. This decrease in amphibiotic conditions in the intertidal zone under the influence of the surf means that as the force and constancy of the surf increase, the vertical stratification of littoral communities becomes decreasingly tied to the tidal levels, since in surf areas they extend higher up the shore than in protected areas. In areas with strong surf, this upward shift may reach 2-6 m (Burrows et al., 1954; Kussakin, 1961; Vozzhinskaya, 1965). Also, as a wave breaks and the layers of water are mixed, the water is enriched with oxygen, frequently to the point of supersaturation. This encourages the existence of many oxyphilic animals in areas where there is surf.

However, the surf also has a harmful mechanical effect, washing away organisms which are not tightly attached. In loose sediments, the surf helps to wash organic matter out of the sediment and causes motion of sediment particles. Therefore, on beaches with surf, even though the oxygen mode is favorable, the food value of the sediment is frequently low.

Depending on the amount of surf action to which a shoreline is exposed, various authors distinguish from 4-5 (Beauchamp, 1914; Lewis, 1964) to 8 (Ballantine, 1961) types of shores. The scheme of degrees of surf action recognized by Soviet investigators of the intertidal zone is as follows (Gurjanova et al., 1930a, b; Kussakin, 1958a, 1961; Gurjanova, 1968).

First degree--closed bays, no surf;

Second degree--partially closed bays, well protected shore, surf very rare and very weak;

Third degree--less protected shore, surf frequent, but weak due to comparatively great distance from open sea;

Fourth degree--open sea, surf almost constant, but not great due to comparatively mild acceleration of waves;

Fifth degree--open sea shore, almost constant strong surf, great acceleration of waves;

Sixth degree--open ocean shore, continuous, strong surf, very great acceleration of waves.

It must be emphasized that the degree of surf action depends not only on the distance of the shore from the open sea, but also on the topography of the shore and morphology of the substrate. If a shoreline is greatly broken, even on an open sea coast, there are always areas which are protected to some extent from the surf. This is observed most clearly in areas of scattered rocky reefs and banks of pebbles and boulders. Even the different sides of a single lump of rock differ in the degree of exposure to the surf and may be populated by different communities.

The composition of littoral communities depends to a great extent on the nature of the sediment. The population of loose sediments depends largely on sediment particle size, mobility, degree of grading, water content in the sediment and the quantity of organic matter present. In surf habitats on loose sediments, there are no macrophytes or almost none, and relatively little microscopic algae. Therefore, the basic food for the inhabitants of sandy beaches, in addition to plankton, consists of allochthonic organic matter (detritus and algae thrown up on the beach). In habitats protected from the surf, where the loose sediment has been silted, there are usually rather rich stands of eelgrass and, in the tropical zone, mangrove as well. In sandy sediments, infauna predominates over epifauna, but in surf habitats it is also quite sparse. Gravel and rocky beaches are still more sparsely populatied.

The population of rocky and stony sediments is significantly more varied. Here, green, brown and red algal macrophytes are usually well developed, with a rich fauna of small mobile animals, plus settlements of sestonophages (barnacles, oysters, mussels). The great biomass of the macrophytes is mostly not eaten by the phytophagous animals; most of it dies and is transformed to detritus. Thus, stony and rocky intertidal zones are distinguished by significantly greater primary production than consumption, whereas the opposite is true of intertidal zones with loose sediments.

On all sediments, particularly rocky sediments, sestonophagous animals (barnacles, bivalves, ascidians, sponges, coelenterata, many higher crustaceans, etc.) are quite important. In the Murman intertidal zone mussels and balani make up 65-90% of the total animal biomass (Kussakin, 1963). Therefore, the role of the pelagic zone as a food resource for the population of the intertidal zone is exceptionally important.

The composition of littoral communities is also influenced by the petrographic composition and morphology of the substrate. It has been shown that changes in the abundance of algae and barnacles are frequently related to variations in the hardness of the rock (Moore, Kitching, 1939). Hard granites and gneisses, even where the surf is strong, can support large Laminaria and Fucuses which attach to them (Gurjanova et al., 1930a, b). Phoronis larvae select primarily sandstone to settle on. When loose soils are close to rocks, this results in silting and accumulation of sand, which also influences the composition of littoral communities. Slightly jointed rock masses, particularly cliffs exposed to the surf, maintain rather homogeneous and relatively sparse populations. The number of bands here is usually minimal, and there are few animals except for barnacles and bivalve mollusks. Conversely, the more broken up the rock, the richer the population it can support. The presence of pools, clefts, niches, overhangs and grottoes creates a variety of conditions of illumination, wetting and protection from the surf. In these areas, the littoral communities are particularly rich and varied. Here we also see a general upward movement of communities into higher levels and movement of certain sublittoral inhabitants into the intertidal zone.

The influence of ice on the littoral biota is both harmful and favorable. The negative influence of ice is primarily a result of its mechanical wearing effect. It is manifested most strongly in an intertidal zone with surf, particularly where the morphology of the coast is simple and the ice is in constant motion. In these areas, the population is entirely destroyed in the winter, then after the ice melts, ephemeral (spring, summer or autumnal) or annual communities develop, with predominance of diatoms and small macrophytes (Chordaria, Pterosiphonia, Polysiphonia, Porphyra, Cladophora, Acrosiphonia). As the wearing effect of the ice becomes weaker, conversely, the significance of communities with predominance of multiannual forms such as laminaria, focuses or Sargasso algae increases (Gislen, 1930; Stephenson, Stephenson, 1954; Kussakin, 1958b). Where the coastline is broken, only individual projecting sections of rock are exposed to the action of the ice. Apparently, the significant changes in the composition of communities observed with various degrees of surf action result not only from the variations in tolerance of plants and animals of the surf itself, but also their resistance to the wearing effects of ice.

On the other hand, an ice cover, particularly where it remains almost immobile throughout the winter, isolates the inhabitants of the intertidal zone from the effects of the very low air temperatures during low tides, and the harmful effects of winter storms. This positive influence of ice cover allows many warm-water species to tolerate severe winter conditions and is, along with the great warming in the summer, one of the main reasons for concentration of thermophilic faunal and floral elements in areas protected from the surf.

Climatic conditions also have a great influence on the intertidal zone. A mild oceanic climate with slight seasonal and diurnal variations in air temperature, cool, wet summers with abundant fog and moderate winters are most favorable for the inhabitants of the intertidal zone. In regions with this type of climate--the Komandorskie Islands, Kerguelen or Macquarie--the intertidal zone is richly populated (Gurjanova, 1935; Ushakov, 1958), since many sublittoral species rise into the intertidal zone. Conversely, in areas with hot, dry summers or cold, long winters, the littoral communities are usually sparse, particularly multiannual algae, which cannot leave the intertidal zone during the unfavorable seasons. Therefore, in the tropics, the algoflora has a tendency to shift downward to the lower horizons of the intertidal zone or into the sublittoral (Gurjanova, 1961a; Mokiyevskiy, 1964, 1967).

The time of day at which low tide occurs is of great significance, particularly in countries with hot, dry seasons (Stephenson, Stephenson, 1972). For example, in the intertidal zone of Ghana in the summer the low tides occur at night, and as a result, regular penetration of certain mass species of algae into higher horizons is observed. In the winter, the lowest tides are observed in the day, resulting in a lowering of the upper boundary of a number of algae (Lawson, 1957, 1966). If fog is frequent during low tide, this has a favorable influence on the littoral biotope. The orientation of the coast is also important, as it determines exposure to sunlight, as is the steepness of the shore. Southern exposures and gentle slopes are more strongly subject to the drying influence of the sun than are northern or steep (i.e., shaded) shores. In countries with monsoon climates, strong rains may cause the death of many littoral organisms if they occur at low tide.

1.3 Typology of Intertidal Zones

In our opinion, the most convenient and acceptable classification of intertidal zones is that based on bionomic types developed by E. F. Gurjanova, I. G. Zachs and P. V. Ushakov (1930a, b). Following the principles which they developed, we can distinguish six bionomic types of intertidal zones.

First bionomic type (moderately protected shore). Characterized by second or third degree surf. Good aeration, salinity usually high, but may be lower near rivers. Distinguished by the greatest richness and variety of littoral communities, the vertical stratification of which coincides most closely with the horizons and stages distinguished on the basis of tidal levels. This type includes many bays, the interiors of certain gulfs, as well as areas of open but broken coastlines protected from strong surf.

Second bionomic type (open sea shore). Characterized by fourth or fifth degree surf. Salinity approximates normal oceanic; conditions of aeration good, water frequently supersaturated with oxygen. The harmful mechanical effect of the surf predominates over the useful effect. The bands of plants and animals are shifted upward, and many of the bands characteristic for areas with weaker surf are absent.

Third bionomic type (open ocean coast). Characterized by maximum surf, strong and constant wetting of entire intertidal zone by spray, even during lowest tide; the harmful effect of the surf is so great that the population is greatly impoverished, but the most enduring forms, having no competition, extend almost throughout the intertidal zone. There is often practically no precise vertical stratification. The communities of the sublittoral edge are shifted upward and occupy almost all or even all of the intertidal zone, while the littoral communities themselves are usually located in the supralittoral zone, which is constantly wet by the surf and spray.

Fourth bionomic type (lagoons). Characterized by total absence of surf (first degree surf) and extensive development of mud and sandy sediments. Salinity usually depressed to some extent, but elevated in countries with arid climate.

Fifth bionomic type (estuaries). Surf usually absent, less frequently second or third degree. Salinity greatly reduced, and usually changes with the phases of the tide. An estuarine intertidal zone is an area in which the continental, marine and fresh-water biota come together.

Sixth bionomic type (pools). We include here all depressions and large indentations in rock, as well as the pools left between rocks and on beaches at low water. This type is characterized by absence of surf or a reduction in the harmful influence of the surf, while retaining its aerating influence, remains quite wet even during the lowest tides, and has a complex hydrologic mode. The temperature and salinity of the water frequently change greatly. One specific feature of pools is that water is constantly present, even if they are located in the supralittoral. This means that the conditions of existence in pools are similar to those of the sublittoral, except that the variations in hydrologic factors are significantly greater than in the sublittoral zone. The main factors determining the composition of the population of pools are their position above the zero depth level, the nature of the sediment, the size and particularly the depth, the effects of wind and surf, the peculiarities of their connection with the sea during low tide (if there is any such connection), the degree of influence of continental runoff, steepness of the walls, nature of change of hydrologic factors and illumination.

Of the many attempts which have been made to classify pools, the classification of T. Gislen (1930) seems most suitable to us. This classification divides them into sublittoral, intertidal zone, and supralittoral types. Sublittoral pools are usually located in the lower horizon of intertidal zones and are usually washed by waves and surf or are connected with the sea by narrow channels. Their population is basically similar to the sublittoral population. Littoral pools are connected with the sea during high tide or when wave action is strong. The changes in temperature and salinity in these pools are significantly greater than in the sea. Their population is usually quite varied; in addition to typical sublittoral and littoral species, forms are also seen which are found only in pools. Supralittoral pools are connected with the sea only during maximum high tide, and sea water enters these pools only in the form of surf spray and storm waves. After strong rains, the water is sometimes almost entirely fresh, while during hot weather, conversely, the salinity may be higher than that of the sea. The temperature fluctuations are also quite great. The fauna and flora of these pools includes a few eurybiotic marine representatives, plus a specific population made up of brackish-water and even fresh-water, frequently ephemeral, species.

Pools are found in all of the other bionomic types of intertidal zones; therefore, many authors do not distinguish them as a specific bionomic type, but rather consider them specific habitats (Newell, 1972) or as separate biotopes (Zhyubikas, 1969) within each of the remaining bionomic types.

1.4 General Characteristics of the Littoral Biota of the World Ocean

We noted earlier that in all climatic zones and on all sediments, clear vertical stratification of organisms is a characteristic of the intertidal zone. On relatively unbroken, morphologically homogeneous shores, the communities are located in bands, strips frequently extending over great distances, but always relatively narrow. They can be easily distinguished on a rocky shore, and are less clearly seen, but still well expressed, on shores consisting of loose sediment. This type of distribution is called linear, or banded.

Some believe (Gislen, 1943; Gurjanova, 1947, 1959, 1961a) that the banded distribution of groups (communities) is primarily characteristic for the intertidal zone in the temperate and higher latitudes, with a mosaic distribution predominating in the lower latitudes. This is explained by the more acute interspecies competition in the tropical intertidal zone, a result of the increased number of species attempting to populate a single level or sublevel (Gurjanova, 1961a). Nevertheless, even in the tropics, the banded (linear) distribution of littoral communities is quite common. On the other hand, even in the temperate zones, where the morphology of the shore is complex, a number of "inserted," supplementary communities appear, and the banded distribution is replaced by a spotty or mosaic distribution.

Along a stony, or particularly rock-cliff intertidal zone, in areas where the shoreline is quite broken, the population is varied. A single rock or column may manifest differences in the quantity, composition and vertical position of the band-forming communities on different sides, with different exposures to the waves. On cliffs extending out into the open sea, the communities are quite different from those on cliffs protected from the surf, and in sections of rock projections located near sandy beaches, the composition of the population is altered in comparison to clean rocks. In areas where fresh water runs down the rocks, the quantity of brown and red algae decreases sharply, the green or blue-green forms becoming dominant. In clefts in the rock, in grottoes or beneath overhangs, communities similar to sublittoral communities develop in abundance, or sponges, Actinea, Ascidia, etc., may be encountered in abundance in these areas alone. On flat reefs with many breaks, large numbers of pools, puddles and depressions are left at low tide. The banded distribution is completely disrupted in these areas, since the pools and depressions have their own communities (sometimes several communities in each pool!), depending on the position of the pool, its depth, the nature of the bottom, etc. Since one or two, less frequently three, species predominate clearly over the others in rocky littoral communities, the appearance of each community can be easily distinguished from the others. Therefore, the variety of the communities is easily seen. In one rocky high boreal intertidal zone in open Kronotskiy Bay, not distinguished either by variety of bionomic types or by richness of species of fauna and flora, in 1970 we found no less than 27 band-forming groups, clearly different as to dominant species.

Thus, for an intertidal zone great changes in communities in the vertical direction and great variability of communities under the influence of local factors are both characteristic. Considering the great local variability, we assume that the littoral biota is almost infinitely variable. Nevertheless, the intertidal zone in almost all regions of the earth, under bionomically similar conditions, supports communities which are of the same type or quite similar, with a limited selection of the very same, either variant or morphologically similar species. As a result, the great variety of littoral communities, upon careful examination, is found to consist of a small number of regularly repeating series of similar communities. Following the lead of botanists (Feldmann, 1951) and certain hydrobiologists (e.g., Dellow, 1950), these series should be called formations.

R. Bolin (1949) believes that the linear distribution of littoral organisms, where almost each individual is peripheral, greatly increases the chances for survival of mutants and gives the organisms high evolutionary potential. This, in his opinion, is one important reason for the tremendous richness of species in the intertidal zone. However, if we exclude the large number of littoraloxene species, which are atypical for the intertidal zone, the number of littoral species is relatively low. On the average, the number of species of animals in an intertidal zone is 1/2-1/4 the number in the upper sublittoral, although the environment there is generally less variable. Apparently, this results from the fact that only the most eurybiotic species can exist in the intertidal zone and supralittoral zones. These species, which have great ecologic plasticity and are polymorphous, i.e., capable of forming various intraspecific (hereditary and nonhereditary) biologic groups, have great evolutionary stability. From the standpoint of the theory of ecologic stability, the eurybiotic species are evolutionarily more stable than the stenobiotic species (Jackson, 1974; Eldredge, 1974).

The following peculiarities of the intertidal zone can be added to those already discussed. It is characteristic for the intertidal zone that the types of communities (formations) are limited, finding homologs and analogs on all coasts of the world ocean. Possible exceptions include the cryocenoses of the Arctic and Antarctic and the mangrove areas of the tropical zone (Golikov, 1975a). These littoral communities consist of a relatively small number of eurybiotic, polymorphous, ecologically plastic but evolutionarily stable species.

These peculiarities of the intertidal zone have been reflected in the figurative words of L. A. Zenkevitch: "The intertidal zones of the various coastlines of the earth represent a play, with the same parts, which are played in different places by different actors."

As to degree of similarity (and in many cases of kinship), littoral communities can be divided into four groups.

1. Identical communities. Groups of organisms occupying similar biotopes within a single biogeographic province or area, less frequently a single climatic zone, the dominant species of which are the same. We must not forget that in terms of its specific composition, one and the same community is far from identical, not only in its remote regions, but also frequently in neighboring regions. In extreme cases, the composition of a single community in different biotopes of a single region may have almost no common species except for the dominant species itself, plus a few banal species common to the entire intertidal zone. For example, on the northwest coast of Iturup Island, a community of *Cystoseira crassipes* algae is found; however, of 17 species of macrophytes which make up the community, only two are common to the cliffs and the rocks, including the band-forming species, and of 45 macrofaunal species, only four are found on both the cliffs and the rocks (Kussakin et al., 1974).

2. Parallel or vicariant communities. Groups of organisms occupying similar biotopes within different zones, biogeographic areas or provinces, with closely related dominant species, usually of one genus, less frequently of one family or superfamily (Thorson, 1957). These vicariant communities frequently dominate throughout an entire biogeographic area. As an example, for the boreal zone we can cite the communities of *Chthamalus stellatus*, *Pelvetia canaliculata*, *Fucus distichus*, *Littorina obtusata*, *Testudinalia testudinalis*, *Gammarus oceanicus* + *Littorina saxatilils*, *Halosaccion ramentaceum*, *Rhodymenia palmata*, *Alaria esculenta* + *Laminaria digitata* on the rocky European coasts and the corresponding communities of *Chthamalus dalli*, *Pelvetia wrightii*, *Fucus evanescens*, *Littorina kurila*, *Collisella cassis*, *Anisogammarus locustoides* + *Littorina sitchana*, *Halosaccion glandiforme*, *Rhodymenia stenogona*, *Alaria angusta* + *Laminaria bongardiana* in the intertidal zone of the fareastern coast of the USSR.

Comparison of the specific composition and biomass of the macrobenthos of the communities of brown algae *Fucus distichus*, characteristic for the middle littoral of the boreal zone in the North Pacific--the lower boreal (southern Kurile) and higher boreal (eastern Kamchatka) zones--shows that, in spite of the fact that eastern Kamchatka and the southern Kurile belong to different biogeographic subareas, the specific composition of the communities of *F. evanescens* is quite similar--54 species are common, something less than 2/3 of the number of species in each of the regions compared, their biomass making up 94-98% of the total biomass of the macrobenthos in the community (Table 1). A quite different picture is observed as we compare the structure of the vicariant communities of *F. distichus* and *F. evanescens* (Table 2). Here, most of the biomass (84-86.5% of total biomass) is accounted for by the vicariant species, although they represent less than half of the total number of species present in the community. The number of common species present is not great, the degree of similarity, as defined by Jnccard, is only 11.8%, increasing somewhat (to 14.6%) if we compare the communities of the higher boreal regions alone.

Table 1. Changes in the composition of the community *Fucus evanescens* in various biogeographic provinces.

Categories of Species	Eastern Kamchatka, higher boreal littoral. Total biomass 4534 g/m^2			Southern Kurile, lower boreal littoral. Total biomass 4879 g/m^2		
	No. of Species	% of total No. of Species	Biomass % of total	No. of Species	% of total No. of Species	Biomass % of total
Species common for both regions	54	62	98(35)*	54	61	94
Vicariant species	16	18	1	18	21	(9)*
Species found only in one region vicariance	17	20	1	16	18	1
Undefined species	-	-	0.1	-	-	5
Total species	87	-	-	-	-	5

*Parentheses show biomass excluding dominant species *F. evanescens*.

3. Convergent or isomorphic communities. Groups of organisms occupying similar biotopes, the dominant species of which are not closely related forms, but belong to the same life forms. For example, in the upper intertidal zone of the tropics, Littorinidae are frequently replaced by Neritidae, while in the middle intertidal zone, the prosobranchial mollusks (of the families

Table 2. Comparison of the structure of parallel communities of *Fucus distichus* and *Fucus evanescens*.

Categories of species	*Fucus distichus* community: coast of Murman. Total biomass 9133 g/m^2			*Fucus evanescens* community: eastern Kamchatka and southern Kurile Average total biomass 4707 g/m^2		
	No. of species	% of total No. of species	Biomass % of total	No. of species	% of total No. of species	Biomass % of total
Species common to both communities	19	31	5	19	16	8
Vicariant species	30	48	84(12)*	42	36	86.5(12)*
Species with no vicariance	13	21	11	57	48	5.5
Undefined species	-	-	0.1	-	-	-
Total species	62	-	-	118	-	-

*Parentheses show biomass excluding the dominant species *F. distichus* or *F. evanescens*.

Patellidae and Tecturidae) are replaced by the externally quite similar pulmonata Siphonariidae.

4. Functionally analogous communities. The dominant species in these communities are not related, and belong to different life forms, but are in the same trophic group. For example, the communities of filter feeders such as barnacles or mussels, common for the intertidal zone, may be replaced by communities with predominance of other filter feeders--sponges, simple *Ascidia* of the family Pyuridae, colonial *Ascidia* of the family Polyclinidae, tubular polychaetes of the family Sabellidae, etc.

1.5 Supralittoral Biota

The population of the supralittoral is extremely homogeneous. For solid sediments, the crustose green and blue-green algae (*Calothrix*, *Plectonema*, *Enthophysalis*) and crustose lichens (*Verrucaria*, *Lichina*, *Lithoicea*, etc.) are typical. The fauna here are mixed in origin. Typical land forms include insects (Machilidae, Staphylinidae, Diptera), pseudoscorpions, red mites, as well as myriopods. The algal wastes contain many oligochaetes. Of the forms of marine origin, most characteristic are specialized families of amphipods, isopods, decapods, and gastropods. Typical are isopods: *Porcellio scaber*, species of the genera *Halophiloscia*, *Detonella*, *Trichoniscus* and particularly the most primitive of the isopods, found only on the sea coast, the Ligiidae (genus *Ligia*). Of the amphipods, for loose soils the Talitridae (genera *Talitrus*, *Orchestia*, *Talorchestia*, *Orchestoidea*) are characteristic. On various soils, gastropods are encountered, primarily the Truncatellidae and Assimineidae (*Truncatella*, *Cecina*, *Assiminea*, *Ovassiminea*, etc.). For the tropical supralittoral on friable soils, the running crabs *Ocypode*, *Sesarma*, etc., land hermit crabs *Coenobita* and representatives of a special suborder of isopods, the Tyloidea (*Tylos*, *Helleria*) are quite characteristic. The *Tylos* species inhabit the coastlines of our seas as well--the Black Sea and Japan Sea.

Clusters of blooming vegetation develop in silty soil, such as the glassworts (*Salicornia*, *Plantago maritima*, *Arthrochemum*, etc.) and, in the tropics, mangroves.

A significant portion of the animals in this zone are scavengers. According to O. B. Mokiyevsky (1969), the biomass and population of species of land origin in the supralittoral are both low, not over a few tenths of a gram per m^2. Groups of marine origin, particularly the Talitridae, provide much of the biomass in the temperate zone: up to 1 kg/m^2, with a population density of as much as a hundred thousand individuals per m^2. In the tropics, the biomass of the Ocypodidae and *Coenobita* is rarely over a few tens of grams per m^2 (Mokiyevsky, 1969).

1.6 Littoral Biota. Rocky Intertidal Zone

The communities of the supralittoral edge in areas with weak or moderate surf usually occupy the upper stages of the highest horizon of the intertidal zone and the lower portion of the supralittoral zone. Most characteristic for this area are the Littorinidae gastropods, and, in the tropics, the Neritidae. Therefore, the supralittoral edge is frequently called the littorine zone. The supralittoral wood lace *Ligia* is also frequently found here.

In the lower boreal European intertidal zone (La Manche, coast of Britain), below the supralittoral zone there is usually a band of lichens of almost black color, dominated by *Verrucaria maura* and *Lichina confinis*. In the lower portion of the lichen band, the quantity of *Littorina neritoides* and *L. saxatilis* increases, as well as mites, the springtails *Petrobius maritimus* and the shore isopods *Ligia oceanica*. Of the algae, in areas of surf, films of blue-green algae develop (*Calothrix*, etc.), plus small green algae and the red algae (*Ulothrix*, *Urospora*, *Bangia*), in places the larger *Porphyra* and *Enteromorpha*. In the lower portion of the supralittoral edge, we always begin to see species characteristic of the upper portion of the eulittoral section: *Pelvetia canaliculata*, *Fucus spiralis*, *Lichina pygmaea*, less frequently *Chthamalus stellatus* and *Fucus distichus* (Lewis, Powell, 1960; Lewis, 1972). In protected habitats, the width of the supralittoral edge is only a few centimeters, but on an open coast, it is greatly expanded by the action of the surf.

On the high boreal intertidal zone of Europe, we do not find *Littorina neritoides* or Ligiidae. On the rocky intertidal zone of Murman, *L. saxatilis* dominates, the amphipod *Hyale prevosti* and oligochaetes are seen. In surf habitat, usually the green algae (primarily *Urospora penicilliformis*), blue-green alagae and a few *Porphyra umbilicalis* are found (Kussakin, 1963). The biomass of algae here is usually not over 200 g/m^2, of animals--1 g/m^2. On the rocky intertidal zone of Murman, the biomass of algae (*Ulothrix pseudoflacca* and *Spongomorpha* sp.) decreases to 30 g/m^2, the biomass of animals increases greatly--to 150-650 g/m^2--due to the increase in the number of *L. saxatilis* (up to 1600 $indiv./m^2$) and the appearance of a large number of amphipods, primarily *Gammarus oceanicus* (>10,000 $indiv./m^2$).

In the northern Pacific in the boreal zone, very similar communities are developed with predominance of *L. sitchana*, *L. kurila* and *L. mandschurica*, gradually replacing each other in that sequence from north to south. On littoral cliffs of the Kurile, the density of *Littorina kurila* reaches 15,000 $indiv./m^2$, with a biomass of up to 2 kg/m^2, while in rocky littoral areas we find up to 100,000 $indiv./m^2$, with a biomass of up to 15.5 kg/m^2.

In the subtropical and tropical latitudes, in addition to the genus *Littorina*, we also find other representatives of the family Littorinidae--*Melarapha*, *Nodilittorina*, *Granulittorina*, *Tectarius*, *Echinella*, *Peasiella*, *Echininus* and *Bembicium*. Sometimes, several species of Littorinidae form independent bands at the supralittoral edge. For example, in Tanabe Bay (Japan), bands of *Nodilittorina pyramidalis*, *N. granularis*, *N. picta*, *Littorina brevicula* and, finally, *Peasiella roepstorffiana* follow in sequence from top to bottom (Habe, 1958). In addition to the Littorinidae, the Neritidae and Grapsidae crabs are also characteristic.

The littoral system per se. This system, in places with moderate or weak surf, is usually located between the mean levels of high water and low water springs or tropical tides and occupies a large portion of the intertidal zone. The population of this system is significantly more varied than that of the supralittoral edge, but here also we encounter only a few formations over a considerable area. Most characteristic are the barnacles (*Chthamalus*, *Balanus*, *Tetraclita*, *Elminius*, *Lithotrya*, *Ibla*, *Octomeris*, etc.), limpets Tecturidae, Patelidae and Siphonoariidae, the predaceous gastropods Thaididae, the mussels Mytilidae (*Mytilus*, *Brachyodontes*, *Modiolus*, *Septifer*, etc.) and the Ostreidae (*Ostrea*, *Crassostrea*, etc.) and the Grapsidae. Usually here we also find Littorinidae and Neritidae, particularly in the upper portion of the system, but here they are rarely among the dominant species. In places, the polychaete Serpulidae or Sabellidae, sea urchins (*Paracentrotus*, *Strongylocentrotus*, etc.), ascidian *Pyura*, etc., may predominate. Among the algae, the green, brown, and red are well represented. In temperate waters, the brown algae usually predominate--the fucoids (in the North Atlantic *Fucus*, *Pelvetia*, *Ascophyllum*, in the northern portion of the Pacific Ocean *Fucus*, *Pelvetia*, *Pelvetiopsis*, in the southern hemisphere *Hormosira*). In warm seas, the red algae usually dominate, and in temperate waters they are numerous in the lower intertidal zone.

The domination of various animals and plants within the intertidal zone itself and their vertical distribution are closely related to their competitiveness and endurance for external factors. The small barnacles Chthamalidae settle higher than the larger Balanidae, and of the latter, such large species as *Balanus cariosus* settle lower than the smaller *B. balanoides*, less capable of competing with the mussel and fucoids.

The geographic vicariate is also rather clearly expressed, although in different oceans the vicariant species have essentially different areas of distribution. For example, *Chthamalus stellatus* extends in the north to Great Britain, whereas its Pacific vicariance *Ch. dalli* extends no further than Olyutorskiy Bay. In contrast, *Pelvetia canaliculata* reaches the shores of Murman, while its western Pacific Ocean vicariance *P. wrightii* extends only to Iturup Island. Many littoral organisms are also asymmetrically distributed with respect to the poles. Thus, Patellidae and Siphonariidae in the northern hemisphere do not extend farther than the lower boreal waters, whereas in the southern hemisphere they are characteristic not only for the Subantarctic, but for the low Antarctic as well.

The lower boreal coast of Europe characteristically features communities of *Chthamalus stellatus* + *Bostrychia scorpioides* and the lichen *Lichina pygmaea*, extending into the uppermost portion of the intertidal zone. The *L. pygmaea* community is among the few littoral communities in which most of the animals feed on the dominant plant. To the north, *Ch. stellatus* is gradually replaced by *Balanoides balanoides*, which settles somewhat lower. Characteristic inhabitants of barnacle communities in the lower boreal intertidal zone of Europe are the *Patella* spp. limpets. In some places, particularly those protected from the surf, the *Fucoidae* dominate, usually forming several bands--*Pelvetia canaliculata* in the upper intertidal zone, then *Fucus spiralis*, still lower *F. distichus* or *F. vesiculosus*. With further weakening of the surf, the Fucusae are frequently replaced by great clusters of *Ascophyllum nodosum*. In the lower portion of the littoral system, a varied community of small algae usually develops, primarily the red algae (*Laurencia pinnatifida*, *Gigartina stellata*, *Corallina officinalis*, *Lomentaria articulata*, *Membranoptera alata*, *Pulmaria elegans*, *Rhodymenia palmata*), as well as brown algae (*Leathesia difformis*, sometimes *F. serratus*). With an increase in surf power, the fucoid cover becomes less prevalent, and the quantity of *Mytilus edulis* increases; in the lower intertidal zone, the brown algae *Himanthalia elongata* and *Bifurcaria bifurcata* frequently dominate. In habitats with heavy surf, the lower portion of the littoral is dominated by lithothamnion, *Balanus perforatus* and *Patella aspera* (Southward, 1958).

The composition of the true littoral communities in high boreal waters of the coast of Murman and the White Sea in its general features is the same, but the species composition is impoverished. The number of bands of fucoids is reduced due to the disappearance of the communities of *Fucus spiralis*, *F. edentatus* and *Pelvetia canaliculata*. The Patellidae are replaced by *Testudinalia tesselata*. In the intertidal zone of Murman, below the supralittoral edge, a community of *Porphyra umbilicalis* + *Balanus balanoides* usually develops, with some green algae *Enteromorpha intestinalis*, etc., *Littorina saxatilis*, *Hyale* *prevosti* and Oligochaetae (Kussakin, 1963). The lower band of *Fucus vesiculosus* is clearly seen only in areas with moderate surf. There are usually few animals--*B. balanoides* and *L. obtusata* predominate. Most characteristic for the true intertidal zone of Murman is the community of *Fucus distichus*. For the lower portion of the eulittoral system, communities of small algae, primarily red algae, are characteristic. They sometimes form a mosaic continuum. The fauna here is much more varied than in the fucoid communities: Between the thallomes of small algae, we find small mollusks, isopods, amphipods, polychaetes, etc. In the habitats below *F. distichus*, protected from the surf, *Ascophyllum nodosum* develops.

Predominance of the same *B. balanoides*, *Mytilus edulis* and fucoids, with the number of bands of the latter in the intertidal zone still less than in Murman, and with some reduction in the number of species, is characteristic for the White Sea. Below the communities of *Porphyra umbilicalis* + *B. balanoides*, there is usually a well developed band of *Fucus vesiculosus*, still lower--a band of *Ascophyllum nodosum*. Of the animals, the mussels usually predominate clearly, while *B. balanoides*, *L. obtusata* and *L. littorea* are also rather numerous.

In the boreal zone of the Pacific Ocean, we find quite similar communities, though more varied in specific composition, although for certain formations (e.g., the fucoids) we find exceptions. The main "characters" here are also the mussels (*M. edulis*, *M. californianus*), the barnacles (*Chthamalus dalli*, *B. cariosus*, *B. glandula*, *B. balanoides* and *B. crenatus*) and the fucoids. The selection of fucoids is not as rich here as in the North Atlantic: *Fucuis evanescens* (similar to the Atlantic *F. distichus*), *Pelvetia wrightii*, *P. fastigiata* and *Pelvetiopsis limitata*.

For the surf intertidal zone of the Bering Sea coast of Chukotka, multiannual algae are typically absent due to the long, severe ice cover. A significant portion of the intertidal zone itself is occupied by the community *Porphyra pseudolinearis* + *Urospora penicilliformis* + Bacillariophyta, while in places communities of *Scytosiphon dotyi* + *Petalonia fascia* + *Pylaiiella littoralis* develop. In the lower portion, we sometimes observe a belt of *Halosaccion compressum* with *H. glandiforme* and *Iridaea cornucopiae* intermixed. Of the animals, oligochaetes predominate, less frequently amphipods. The biomass of animals is never over 20 g/m^2.

The intertidal zone of Anadyrskiy Bay is quite poor, both qualitatively and quantitatively, but further to the south, in the direction of Olyutorsky Bay, the arid zone is gradually enriched and takes on features characteristic for a high boreal intertidal zone in the far eastern seas. The intertidal zone of eastern Kamchatka is populated quite richly and can be characterized as a typical high boreal intertidal zone of the northwestern Pacific (Spasskiy, 1961). The high boreal type of intertidal zone is also well represented by a large portion of the coast of the Sea of Okhotsk, south to Cape Terpenia and Friz Bay, and also along the Pacific coast of the Kurile to the south to Yekaterina Bay. The intertidal zone of the individual sections of the continental coast of the Sea of Okhotsk has been described by P. V.

Ushakov (1951) and O. B. Mokiyevskiy (1953), of the Shantarsky Islands--I. G. Zachs (1929). For the upper portion of the intertidal zone itself in the northern Sea of Okhotsk, bands of *Gloiopeltis furcata* and *Heterochordaria abietina* + *Myelophycus intestinale* with a sparse fauna consisting primarily of *Littorina sitchana* and *Chthamalus dalli*, and particularly, settlements of barnacles--*Ch. dalli*, *B. crenatus* and *B. balanoides*--are most characteristic.

Extensive development of banks of *Mytilus edulis* are a characteristic feature of the littoral of the continental coast of the Sea of Okhotsk, giving it features of external similarity to the White Sea intertidal zone. The number of mussels is usually great among stands of fucus, but the clusters of mussels descend to horizon III, where they are frequently quite dense. In addition to the mussels, settlements of fucus are often seen in the lower portion of the eulittoral system, while the formation of varied, usually mosaically arranged small algae, primarily red and brown algae, is most common. The biomass of plants in the communities of the upper portion of the eulittoral is 150-800 g/m^2 in stands of *Gloiopeltis capillaris*, 250-800 g/m^2 in the band of *Heterochordaria abietina* + *Myelophycus intestinale*, up to 3-4 kg/m^3 in the group of *Porphyra ochotensis* and up to 5 kg/m^2 in the band of *Halosaccion glandiforme* (Vozzhinskaya, 1965, 1967; Blinova, Vozzhinskaya, 1974). An equally high plant biomass is seen in associations of fucus, *Corallina pilulifera* and various red algae--up to 4-9.5 kg/m^2.

In the northern and central Kurile, in the upper portion of the littoral system, communities of *Gloiopeltis furcata*, *Porphyra umbilicalis*, *Acrosiphonia*, *Blindingia*, *Monostroma*, and in places *Heterochordaria abietina* usually develop. Barnacles do not settle here. Most characteristic for the middle portion of the system are stands of *Fucus evanescens*, or if the surf is strong--*Balanus cariosus* settlements with biomass of up to 21 kg/m^2 (Kussakin et al., 1974). Slight development of *Mytilus edulis* is characteristic. For the lower portion of the littoral system, the red algae *Rhodymenia stenogona*, *Rhodomela larix*, *Rhodoglossum japonicum*, *Iridaea cornucopiae*, *Ptilota asplenioides* are characteristic, while the characteristic animals are the gastropods *Littorina kurila*, *Lacuna reflexa*, *Nucella freycineti*, *Buccinum percrassum*, *B. baeri*, *Collisella* spp., primarily *C. cassis*, the bivalves *Vilasina vernicosa*, *Turtonia minuta*, the polychaetes *Nereis vexillosa*, *Chone teres*, the crabs *Pagurus hirsutiusculus* and *P. middendorffi*, the isopods *Idotea aleutica* and a large number of amphipods. In the middle Kurile, hermit crabs and isopods are absent.

In the southern Kurile, southern Sakhalin and the northern portion of the Japan Sea, right down to Nevel'skiy Bay, the intertidal zone is of lower boreal type. The overall appearance of the communities of the eulittoral is retained, but it is characteristic that the upper portion of the system contains bands of *Chthamalus dalli* and the fukoid *Pelvetia wrightii*, while the lower portion features certain warm-water algae. There is a gradual disappearance of the high boreal species, replaced by vicarious low boreal species. Furthermore, general enrichment of the specific composition of the fauna is observed. The peculiarities of the low boreal intertidal zone are most clearly expressed along the coast of southern Primor'ye, where the tidal range is short, and where Fucus evanescens disappears, and Pelvetia wrightii becomes more rare. Most characteristic for the upper portion of the littoral are Littorina mandshurica and L. brevicula, a band of Gloiopeltis furcata, sometimes forming mixed stands with H. abietina, and a band of Chthamalus dalli, while in the lower section we see mosaically distributed stands with predominance of red algae.

The high boreal intertidal zone of the Pacific coast of America has a great deal in common with the high boreal intertidal zone of Asia. However, due to the less severe winter conditions here, there is a significant influx of warm-water species, e.g., the crabs Pugettia, Oregonia and Cancer. The high boreal intertidal zone, characteristic, in particular, for the Aleutian Islands and the Gulf of Alaska, begins to be replaced by a low-boreal intertidal zone (much more gradually than along the coast of Asia) around Vancouver Island and the northern portion of the coast of the state of Washington. The typical low boreal intertidal zone of northern California extends with slight variations to Cape Conception (Ricketts, Calvin, 1961; Stephenson, Stephenson, 1972).

In southern California, the intertidal zone is of subtropical type, although with some boreal aspects, a result of the relatively cold water which washes this coast even in summer. The southern features are introduced with settlements of the gastropods Vermetidae--Spiroglyphus lituellus and Altes squamigerus, the relative abundance of the trochids Norrisia, Tegula funebralis, T. ligulata, the turbinids straea undosa and the bivalve mollusk Pseudochama exogyra. Calcareous red algae are also abundant in the lower portion of the intertidal zone.

Along the coast of Asia, the lower boreal intertidal zone extends to the south approximately to Cape Inubo and Sado Island along the coast of Japan and to Wan San along the coast of Korea.

Along the northwestern coast of Honshu Island, the intertidal zone is a transient type between low boreal and subtropical, the boreal Chthamalus dalli being replaced by the subtropical Chthamalus challengeri (Hoshiai et al., 1965). The intertidal zone of Sagami Bay on the Pacific coast of Honshu is of subtropical type, although there is some intermixture of boreal species and genera, e.g., Strongylocentrotus (Gislen, 1943). Of the barnacles, Balanus amphitrite and Tetraclita squamosa are characteristic for the uper portion of the intertidal zone, of the algae--Monostroma, Sargassum thunbergi and Turbinaria, for the lower portion--Chondrus + Gigartina, still lower--Corallina + Pachyarthron + Laurencia with the characteristic craboid Petrolisthes Japonicus. A community of Ch. dalli is still retained on the rocky intertidal zone of the Yellow Sea, but is mixed with many subtropical species. Lower down are belts of oysters and ulva algae (Gurjanova et al., 1958). In the eastern China Sea, we observe massive development of warm-water cirripedian crustaceans Tetraclita squamosa and Mitella mitella (Mokiyevskiy, 1967). In the southern China Sea on shores with surf and high salinity, coral reefs develop, though they are sparse. The remains of ancient colonies of coral which have died are still more commonly seen.

Further south, along the cliffs of the Indo-China peninsula, in the upper portion of the intertidal zone there are few algae, but a rich population of settled animals (actinea, serpulids, the barnacles Tetraclita porosa, Balanus and Chthamalus, complex ascidians, the oysters Ostrea forskali and O. spinosa), and in the lower portion the algae Turbinaria, Padina, sargassums and calcareous red algae such as Melobesia develop (Fischer, 1952).

In Indonesia, the Nerita rise quite high in the intertidal zone. The distribution of fauna is quite variegated and mosaic. The overwhelming portion of the intertidal zone carries low biomass--a few grams, less frequently a few tens of grams per m^2 (Mokiyevskiy, 1967).

Along the coast of northern and northeastern Australia, there are extensive coral reefs extending into the intertidal zone. In the upper portion of the intertidal zone itself are settlements of Chthamalus malayensis and Ch. withersii with occasional isopods. Below this are bands of Crassostrea amasa, Tetraclita squamosa and a narrow band of Acanthozostera and Liolophura or Acanthopleura. Still lower we see the simple ascidians (Microcosmus australis), Chthamalus caudatus, Tetraclita costata, sponges, Siliquaria ponderosa, crabs, holothurians and the algae Valonia and Padina (Stephenson, Stephenson, 1972). In southern Australia and Tasmania, settlements of Chamaesipho columna, Chthamalus antennatus and Catophragmus polymerus develop, plus bands of Modiolus pulex and Brachyodonte rostratus. In the lower portion of the intertidal zone there is usually a band of Galeolaria caespitosa (Bennet, Pope, 1953).

Along the intertidal zone of the Subantarctic island of Macquariae, there are apparently no barnacles; the most characteristic vegetation is Porphyra umbilicalis with some Ulva lactuca, Enteromorpha intestinalis and other algae. The lower portion is dominated by Rhodymenia. Of the animals, the gastropods Siphonaria lateralis, Nacella delesseri and Macquariella hamiltoni are most common (Stephenson, Stephenson, 1972).

The sublittoral or infralittoral edge. This level usually occupies the lower portion of the zone which dries out, and when the surf is weak corresponds to the lower stage of horizon III of the intertidal zone. Independent communities are formed rather rarely here; more frequently, communities of the upper sublittoral simply extend into the zone. However, due to the drying of the edge, though it may be brief, its population differs from the sublittoral population; first of all, the specific composition is much more sparse. Secondly, certain strictly littoral species are present. In cold and temperate waters, large laminaria algae predominate, while in warm waters we usually see the upper boundary of the colonies of corals, dense clusters of the ascidian Pyura, and stands of Sargassums and red algae are encountered; at all latitudes, calcareous Rhodophyta are seen here, belonging to various genera, but usually called lithothamnion (cortical and branched, nonsegmented forms) and corallina (branched segmented forms). Frequently, in warm waters, these calcareous red algae develop quite rapidly and form massive "bridges" or "trotoires" (in the Mediterranean) or even entire reefs (in the tropics). The porous or spongy thallomes of these plants provide shelter for numerous cryptofauna. In warm waters, calcareous

Chlorophyta are also common, for example, *Halimeda*, but their significance in the formation of reefs is much less. In rocky places, communities of sea grasses (e.g., *Phyllospadix* in the northern Pacific) are found, although they are more characteristic for looser beds. On the whole, the sublittoral edge is the most varied portion of the intertidal zone in terms of specific composition. It is here that we find significant numbers of species from the groups of animals which are not characteristic for the intertidal zone, as are the Echinodermata, *Ascidia*, sponges, Bryozoa, Cephalopoda, Brachyopoda, fish, etc.

In the boreal intertidal zone of the Atlantic Ocean, the development primarily of laminaria algae, to a lesser extent red algae and fucuses, is characteristic. Of the animals, the most common are *Mytilus edulis*, the gastropods *Testudinalia tessellata*, *Littorina littorea*, *Nucella lapillus*, the sea urchens *Strongylocentrotus droebachiensis*, the sea stars *Asterias*, the sea anemone *Tealia*. Where the surf is weak, the laminaria are frequently replaced by *Fucus serratus* stands.

The high boreal eastern Atlantic sublittoral edge is quite poor in species composition. For example, the Patellidae are practically absent here. Nevertheless, the main band-forming species remain the same: *Alaria esqualenta*, *Laminaria digitata*, *L. saccharina*, *Mytilus edulis*, *Fucus serratus* and the Rhodophyta.

In the northern Pacific, fucus is absent in the sublittoral edge, but the zone of laminaria is usually well developed. In surf intertidal zones of the Bering-Sea coast of Chukotka, typical communities of the sublittoral edge are not found; only associations common with the intertidal zone of seasonal and ephemeral algae develop here. In the intertidal zone which is protected from the surf in Krest Bay, a community of *Laminaria bongardiana* appears, and extends to the south along Kamchatka, the northern and middle Kurile. Along the coast of eastern Kamchatka, in places there is a well expressed band of *laria angusta*, while on the northern and central Kurile there is also a community of *Laminaria longipes* and *Cymathaere triplicata*.

On the littoral coast of the Sea of Okhotsk, the composition of macrophytes of the sublittoral edge is quite different--*Laminaria longipes* and *Alaria praelonga* are characteristic only for southwestern Kamchatka, while further to the north and west, *Lessonia laminarioides*, *Laminaria gurjanovae* and *L. saccharina* are most typical. It is interesting that *Cystoseira crassipes* is also present, although most of its stands are located in the sublittoral (Vozzhinskaya, 1965; Blinova, Vozzhinskaya, 1974). In the lower boreal intertidal zone of the southern Kurile, in addition to the laminariaceans *Kjellmaniella gyrata*, *Costaria costata* and *Arthrothamnus bifidus*, stands of *C. crassipes* are quite widespread and, to a lesser extent, *Sargassum kjellmanianum* and *S. thunbergi*, while on the coast of southern Skhalin we find *C. crassipes*, *Sargassum pallidum*, *Laminaria cichorioides*, *L. japonica* and *Alaria marginata*. Stands of *Phyllospadix iwatensis* are also characteristic for both of these regions. Along the continental coast of the Sea of Japan, laminariaceans extend into the intertidal zone only in places in northern Primorye, *Phyllospadix* and Sargassums being characteristic only for the upper sublittoral, while the sublittoral edge is populated primarily by a mosaic of algae with predominance of Rhodophyta, as well as some brown algae, particularly *Coccophora langsdorffi*. It is here that the stands of lithothamnions usually begin, the thickness of the cover of which gradually increases in the sublittoral with increasing depth. The animals here are more varied. Particularly noted is an increase in the number of echinoderms: the stars *Henricia* and *Leptasterias*, *Strongylocentrotus*, the holothurians *Cucumaria*, etc. Of the decapodes in the intertidal zone of eastern Kamchatka and the Kurile, *Thelmessus cheiragonus* is characteristic, as well as juvenile *Paralithodes brevipes*, etc. In the quantitative aspect, on the boreal edge, it is not animals but plants which dominate. Only in the baths of the Komandorskiy and, to some extent, the Kurile, does *Strongylocentrotus polyacanthus* form rich accumulations, though on reefs, frequently covered with sand, populations of the sabellids or ascidians develop, with almost no algae.

Along the Pacific coast of North America, the sublittoral edge is richly populated with laminaria such as *Alaria valida*, *A. marginata*, *Egregia menziesi*, below which we usually find *Lessoniopsis littoralis*, and still lower--the sublittoral gigantic *Nereocystis leutkeana*, *Macrocystis pyrifera* and *M. integrifolia*. Also characteristic are *Sargassum muticum*, *Cystoseira crassifes*, *C. osmundacea* and *Phyllospadix scouleri*. Among the red algae, the most common are species of the genera *Iridophycus*, *Gigartina* and *Odonthalia* (Stephenson, Stephenson, 1972).

In the temperate waters of the southern hemisphere, large brown algae such as *Durvillea antarctica*, *D. willana*, *D. potatorum*, *D. caepestipes*, *Lessonia corrugata*, *L. nigrescens*, *Macrocystis pyrifera*, species of *Cystophora* and *Carpophyllum* also develop.

A somewhat poorer laminarian flora is found in the subtropical waters of both hemispheres, e.g., in southern California, Japan, South America and southern Australia (species of the genera *Eisenia* and *Egregia*). However, most characteristic for the warmer waters are the calcareous red and green algae, and of the brown algae--*Sargassum*, *Turbinaria*, *Dictyota* and *Padina*; therefore, the appearance of the lower portion of the intertidal zone is quite different from the intertidal zone in the temperate waters. This difference is increased still further by the departure of the coral or algal reefs or accumulation of Vermetidae and the Polychaetae serlupids *Pomatoleios* and *Pomantoceros*, inhabiting the calcareous tubules of the gastropod mollusks (Southward, 1958).

1.7 Characteristic Peculiarities of the Littoral Biota of the Tropics and Circumpolar Waters

Until recently, it was widely thought that, as we move toward the tropics, a general tendency is observed toward descent of the littoral fauna and flora into the deeper horizons and the sublittoral and, in connection with that, a general impoverishment of the littoral biota (Gislen, 1943-1944). The studies of E. F. Gurjanova (1959, 1961a, 1961b) and O. B. Mokiyevskiy (1960, 1964, 1967) have shown that this impoverishment may be true only of algae, whereas only a few species of animals descend in the tropics, and the indices of quantitative development of species and biocenoses are almost equal to those of the temperate latitudes, and in many cases even higher. The rule of domination of one or a few species is retained in the tropical biocenoses, but at a lower quantitative level (Mokiyevskiy, 1964). As we move toward the tropics, the specific variety of Rhodophyta and most groups of animals increases, particularly for the crabs, sea urchins, sipunculoids, polychaetes, gastropods and bivalves, etc. Furthermore, a number of systematic groups of high rank, such as Pennatularia, Scleractinia, Alcyonaria, Zoantharia, hingeless Brachiopoda, Xiphosura, Stomatopoda and Crinoidea inhabit the intertidal zone only in the tropics. Conversely, some large systematic groups which inhabit only the temperate zones are absent (Mokiyevskiy, 1962). Only a few groups of animals, such as the amphipods and isopods, are present more richly in the temperate waters than in the tropics. In the opinion of O. B. Mokiyevskiy, the combination of conditions present in the tropical intertidal zone results in a complex interweaving of biocenotic connections between organisms, preventing the realization of short and, consequently, energetically more effective food chains such as are inherent in the biocenoses of the boreal and, particularly, high boreal intertidal zone.

As we move toward the Arctic and Antarctic, gradual qualitative and quantitative impoverishment of the littoral biota occurs, to the point of complete disappearance in the high Arctic and along a large portion of the coast of Antarctica. Since the harmful, wearing effect of long-term ice cover is particularly strongly felt in the intertidal zone with its surf, the impoverishment in the Subarctic is more strongly seen in intertidal zone areas with surf than in areas with little or no surf. This is clearly seen in the example of Anadyrskiy Bay. Whereas on the rocky intertidal zone with heavy surf the biomass of plants varies from 0.2 g/m^2 in a community of *Urospora penicilliformis* to 3.8 kg/m^2 in a community of *Halosaccion compressum*, while the biomass of animals is only 0.5-40 g/m^2 in the intertidal zone of Provideniye Bay and Krest Bay, which are protected from the surf, the biomass of plants varies from 88 g/m^2 to 11.2 kg/m^2, while the biomass of animals may reach 13.5 kg/m^2. The clear impoverishment of the littoral biota in Subarctic-type surf habitats occurs primarily due to the complete disappearance of perennial plants and sessile animals. That moving ice is the culprit in this impoverishment is demonstrated by the fact that in summer, stands of fucus or barnacles less than one year old frequently appear here, but mature individuals remain only in clefts and other protected habitats. Seasonal species of algae predominate in the intertidal zone (apparently, the green filamentous algae and diatoms extend furthest north), along with small, mobile animals, capable of concealing themselves in the mats formed by these plants--amphipods, oligochaetes, small polychaetes, nematodes, acarines, ostracods, harpacticoids. The mobile multiannual forms of macrobenthos also continue to play some role (*Testudinalia*, littorines, nudibranchs, sometimes sea stars, sea urchins and hermit crabs), which winter in the sublittoral or in concealed places. Still closer to the Bering Straits, the population is severely depressed, even in areas protected from the surf. Here, the entire littoral zone is covered with ice for several months each year, and the few multiannual forms which penetrate here, such as Fucus evanescens, Mytilus edulis, Tectonatica janthostoma, Balanus crenatus, leave the dry zone and descend into the sublittoral.

Similar changes in the littoral biota upon transition from the boreal to Arctic conditions have been obsevrwed on the Atlantic coast of North America, in Greenland (Madsen, 1936) and in the Barents Sea (Gurjanova et al., 1925). For example, in southern Greenland in the intertidal zone itself, the zone of Balanus balanoides with bands of Fucus vesiculosus in the upper portion and F. distichus + Ascophyllum nodusum + Mytilus edulis in the lower portion are still clearly expressed. Further to the north, A. nodosum is absent, B. balanoides becomes rare and also gradually disappears, the laminarians in the infralittoral edge are replaced by mats of small algae. Along the northeast coast of Greenland, of these multiannual forms, only F. distichus remains, and it also is rare (Madsen, 1936, 1940). In the eastern Barents Sea, a gradual impoverishment of the littoral biota occurs from west to east. Along the west coast of Novaya Zemlya, there is still a great deal of Fucus evanescens. In the central portion of Matochkin Shar strait, multiannual macrophytes disappear completely from the intertidal zone and bands of Urospora penicilliformis (upper) and Pylaiella litoralis (lower) are seen. Along the coast of the Kara Sea there is no macrophyta, and only at depths of 4-6 m do we see individual Fucus distichus among the stands of laminarians.

Information on the littoral life in the Arctic itself is sparse, and the data available are quite contradictory. Some authors report that the intertidal zone here is completely lifeless, while others report rather significant numbers of species of macrobenthos for the coastal zone. It is most probable that only cryocenoses are present in the Arctic intertidal zone.

The impoverishment of the littoral biota in the Subantarctic and Antarctic occurs similarly, though with some differences. In the southern hemisphere, representatives of the family Patellidae penetrate clear to the Antarctic peninsula, whereas in the northern hemisphere they are almost totally absent even in the high boreal waters. Barnacles disappear in the Subantarctic. The intertidal zone of most of the coast of Antarctica is apparently totally lifeless. The poor population is observed only in the Antarctic peninsula and adjacent islands, as well as Adelie land. In the intertidal zone of the Antarctic peninsula, the tides are as great as 3-4 m, and in the summer along the supralittoral edge, orange (Caloplaca) and black (Verrucaria) lichens develop, in the eulittoral zone--stands of Chlorophyta Ulothrix, Urospora, Monostroma, Enteromorpha, Cladophora, Chaetomorpha and the Rhodophyta Bangia and Porphyra (Delepine, 1966). Phytophyllic gastropods Margarella, Nacella and Patinigera polaris are found. In places protected from the wearing effects of the ice, a rather varied population is observed with predominance of the small bivalve mollusk Kidderia subquadratum, which reaches a distance of 75 cm over the zero depth level under the cover of the algae Iridaea racovitzae (Stockton, 1973). In the region of Adelie land, where the conditions of habitation are still more severe, the supralittoral edge is also populated with lichens, apparently of the same species. Only two bands are clearly seen in the intertidal zone: the upper band, formed of *Ulothrix australis*, and the lower band of diatoms, predominated by *Melosira moniliformis*. Macrophytes appear only in the sublittoral (Delepine, Hureau, 1963). It is interesting to note that most genera of algae in the Antarctic intertidal zone are the same as in the Subarctic regions.

1.8 Sandy and Silty-Sandy Intertidal Zone

In the qualitative aspect, loose soil beds are significantly more sparsely populated than solid beds. The population of sandy beaches exposed to surf is particularly sparse and homogeneous. Under Subarctic conditions, the macrofauna is usually absent, although the meso- and microfauna are rather widely varied. For beaches with surf in the temperate and tropical zones, the most characteristic of the macrofauna are the higher crustaceans: amphipods, isopods and, in the tropics, crabs as well. Macrophytes are absent here, only microscopic algae being present, rising to the surface of the sand for photosynthesis at low tide and burying under the sand at high tide. As to composition of fauna, three systems are usually distinguished on sandy beaches with surf--the splash zone, or upper beach, which may be combined with the supralittoral edge of a rocky intertidal zone; the middle beach, occupying a significant, sometimes predominant, portion of the intertidal zone, and frequently poorest in life; the lower beach, in the lowest portion of the intertidal zone. For the splash zone, the amphipods Talitridae (*Orchestia*, *Talorchestia*, *Orchestoidea*) are characteristic. In the tropics, the Ocypodidae predominate, constructing deep burrows and running after the retreating waves with surprising speed. In warm seas, right up to the lower boreal subzone, isopods of the suborder Tyloidea (*Tylos* and *Helleria*) are common. The middle beach in the high boreal waters is quite poorly populated. Most characteristic are the sand hoppers (*Gammarus* and *Anisogammarus*), the turbellarians, oligochaetes and nematodes. Primitive isopods of the family Cirolanidae (*Excirolana*, *Eurydice*) appear in the lower boreal intertidal zone; and are particularly characteristic for the tropics and subtropics. Less common here are the polychaetes *Euzonus*, *Ophelia*, *Scolelepis*, *Nerine*, *Goniadides* and others. The lower beach is usually populated with a more varied and richer fauna. Most common here are the amphipods of the family Haustoriidae and Phoxocephalidae. For the tropics, crabs of the family Hippidae (*Emerita*, *Hippa*, *Arenaeus*, etc.), the bivalve mollusks *Mesodesma*, *Amphidesma*, *Donax*, the gastropods *Terebra*, plus the crustaceans *Squilla* and *Callianassa* are typical. For both the warm and temperate waters, the predaceous gastropods of the family Naticidae, the bivalves *Tivela*, *Tellina*, *Siliqua*, polychaetes of the family Nephthydidae, Glyceridae, Ariciidae and Opheliidae, mysids and isopods of the family Cirolanidae are characteristic. Many of these species are found not so much in the lower intertidal zone as at the water line, i.e., they form a migrating complex (mysids, many Cirolanidae, *Donax*, some amphipods, shrimp, etc.). The biomass of animals on sandy surf beaches is usually low, although in some places it may be significant.

As the surf weakens, the population of the sandy beaches becomes significantly richer, particularly in the lower portion. The leading groups are usually the bivalves (Veneridae, Cardiidae, Mactridae, Tellinidae, Myidae) and polychaetes (Cirratulidae, Opheliidae, Maldanidae, Terebellidae, Phyllodocidae, Glyceridae, Eunicidae, Capitellidae). Among the gastropods, both predators and scavengers are common, particularly Naticidae (*Natica*, *Tectonatica*, *Acrybia*, *Polinices*, etc.). There are also large numbers of crustaceans: in the upper intertidal zone, the crabs and amphipods-talitrides, in the middle and lower intertidal zone--the sand shrimp Crangonidae, decapod crustaceans *Upogebia* and *Callianassa*, Squillidae, the isopods Sphaeromatidae, less frequently Cirolanidae. Macrophytes begin to appear here, particularly in the tropics--*Caulerpa*, *Udotea*, *Halimeda*, etc.

In temperate waters, most of the algae do not use sand as the substrate, but rather shells, rocks or pebbles, while some species, such as *Cladophora fracta* in the White Sea, simply rest on the sand, but are not attached to it.

Still further weakening of the surf, observed in partially closed bays, lagoons and estuaries, is accompanied by silting of the sand and freshening of the water. In countries with arid climates, lagoons become brackish. For estuarine and lagoon types of intertidal zone, the Potamogetonaceae and Hydrocharidaceae are more common than algae. Among the genera of the first family, *Zostera* is most widespread, while *Posidonia* grows in the Mediterranean, and in the tropics--*Cymodocea*, *Halodule* and *Althenia*. Representatives of the second family, such as *Halophila*, *Thalassia* and *Enhalus*, grow only in the tropical seas. The infauna in stands of eel grass consist primarily of the same groups as are found on sandy beaches with weak surf, but a unique fauna settles on the leaves of the grass, containing both common phytophilic forms (Trochidae, Turbinidae of the gastropods, *Vilasina* of the bivalves, etc.) and species which are specially adapted for life on the leaves of marine grasses, e.g., the isopod *Idotea rotundata*, mollusks such as the limpets *Siphonacmea oblongata* and *Collisella angusta*.

In addition to the sea grasses, mangroves are also found in the tropics. These are ancient plants, which have adapted to life along the sea shore. Mangrove stands are low (up to 5-10 m) evergreen groves, rising from silty shores protected from the surf. The adaptation of the mangroves to life in an amphibiotic medium on muddy, semiliquid silt under conditions of physiologic dryness has been to develop stiltlike roots which can survive in the air, pulpy leaves with watery stoma, through which the excess of salts is excreted, reservoirs of fresh water in old leaves and air-carying tissues in the fruit, allowing it to float. Mangrove stands are common in the tropics and extend into the subtropics from 35°N to 37°S. Most common are representatives of the genera *Avicennia*, *Rhizophora*, *Sonneratia*, *Laguncularia*, *Bruguiera* and *Ceriops*. Mangroves are the pioneers in the colonization of silty estuaries by land plants and the advance of the shore into the sea. Populating the brackish silts, suitable only for a very few halophiles, they facilitate consolidation of the bed and its gradual transformation to soil. In this way, they gradually create the prerequisites for the formation of a tropical forest. The distribution of mangrove stands is usually stratified. For example, in southern Florida *Rhizophora* is located along the lower boundary of the intertidal zone, then, closer to the shore, *Avicennia* is seen. In the tropics, there are as many as five zones. The fauna of mangrove stands is not distinguished by great variety, particularly the infauna, which is primarily a result of the shortage of oxygen in the semiliquid ooze. Most characteristic are the crabs Portunidae, Grapsidae, Ocypodidae, many of which construct burrows, expelling a plug from the soil; the fish are the *Periophthalmus* and *Boleophthalmus* and the Gobiidae, and the gastropods Neritidae and Littorinidae (particularly *Littopinopsis*) are present, as well as oysters, and certain polychaetes. Many animals utilize the leaves and trunks of the mangroves as substrates. The invertebrates are dominated by detritophages, sestonophages (cirripedia and oysters) being encountered only in the lower portion of the intertidal zone (Sasekumar, 1974).

In the temperate zone, in low places protected from the surf, salt meadows or marshes are frequently formed. In contrast to mangrove stands, marshes are not located in the intertidal zone, but above it, and only certain halophilic plants frequently occupy the upper portion of the littoral zone. The lower portion of the intertidal zone is either populated with eel grass (*Zostera*) or contains no macrophytes at all. This type of silty-sandy littoral below the marsh zone is referred to as the tidal marsh. Mangrove stands and stands of halophilic plants are different formations with different abiotic and physionomic features. The only similarity is that the halophilic grasses and their fauna and algoflora also consolidate the semiliquid bed and facilitate its gradual conversion to soil. The pioneer of the higher plants in the upper intertidal zone and in the sublittoral in temperate waters is usually the halophyte *Salicornia*. The bonding of silt particles is facilitated by the *Corophium volutator* amphipods and the mucus-liberating algae which settle here. The halopohytes are followed by multiannual plants such as *Puccinella maritima*, plus other salt-tolerant species which settle on the substrate which they prepare: *Aster trifolium*, *Plantago maritima*, *Armeria maritima*, etc.

Sandy, silted shoals, not subject to strong wave action, are significantly more productive than open sandy beaches, which are poor in detritus. Whereas the surf zones of sandy beaches are dominated by euryphages, which can feed on fresh and decomposed plant and animal residue, as well as living animals, silty-sandy shoals can support a large number of detritophages which swallow the soil of the bed and sorb detritus from the surface increases sharply. Silty shoals, completely protected from the surf in some estuaries, lagoons and closed bays are still more richly populated; in addition to the infauna, rich epifauna develops, represented by the Littorinidae, Potamididae, mussels and oysters, on which barnacles and other epifauna can develop and, in the tropics, crabs, sea cucumbers and sea urchins.

The greatest biomass is that of the sestonophages--the mussels and oysters, which frequently form continuous settlements. Most of the remaining representatives of the epifauna collect detritus from the surface of the bed. Various species living in the mass of the bed burrow into it to various depths and thus utilize the nutrient resources of the various layers of the bed.

Under subarctic conditions, and to some extent under the conditions of the high boreal subzone, extensive, heavily silted spaces in the estuarine intertidal zone are quite sparsely populated, with macrophytes frequently absent, while the sparse macrofauna are represented primarily by the amphipods and *Mesidotea enotomon*.

The biomass of the mussels and oyster banks (almost exclusively animal) reaches several kilograms per m^2. A significant biomass (up to a few kilograms per m^2) is also found in stands of marine grasses, mostly plant biomass. In the remaining communities, the biomass is significantly lower and reaches a few tens or hundreds of grams per m^2, both in the tropics and in the temperate zone.

2. The Communities of Coral Reefs. (Yu. I. Sorokin)

The biogeocenoses of coral reefs represent one of the most active biologic systems in the world ocean, and in fact, on the planet as a whole. The area occupied by coral reefs only in the Pacific Ocean is comparable to the area of the continent of Australia. The biological activity of the coral biogeocenoses, per unit area, is 20-100 times greater than in the pelagic areas of the tropical zone of the oceans. For example, the daily primary production of photosynthesis in the coastal waters is 0.15-0.30 g C/m^2, whereas in coral communities of the phytobenthos, periphyton and symbiotic zooxanthellae, it is 5-20 g C/m^2. The activity of the microflora, characterized by its destructive activity and heterotrophic production in the coral biogeocenoses is 10-20 times higher than in the surrounding oligotrophic tropical waters.

The processes of biogeochemical circulation of matter occur in coral reef ecosystems much more intensively than in the surrounding tropical waters and on the ocean floor. It is quite probable that it is in the coral communities that microbial oxidation of the fraction of organic matter resistant to sea water occurs (Sorokin, 1971a). Due to the high productivity, optimal oxygen mode and high temperature of the water in coral communities and in the regions of the surrounding shelf, optimal conditions are created for the breeding and feeding of many species of commercial animals.

Coral reef communities in and of themselves represent a classic example of a biogeocenosis as a self-supporting community, which creates its own physical substrate and chemical medium. At the same time, coral biogeocenoses are distinguished from the surrounding oligotrophic waters and exist basically on the energy of autochthonous primary production. The system is organized so that the absolute concentration of nutrients is maintained at a high level, in spite of an intensive exchange with the surrounding oligotrophic waters of the ocean. The biological mechanisms which maintain the reserves of nutrients and a high productivity of the coral communities--conditions of an intensive physical contact with the oligotrophic waters which pass over the reef--represent an interesting problem. Its interpretation will doubtless be of important significance in the creation of a theory of marine aquaculture and will thereby assist in the solution of one of the key problems of modern hydrobiology.

Primary production in coral communities is basically created by the photosynthesis of hermatypic reef-forming organisms. The processes of sedimentation of $CaCO_3$ and $MgCO_3$ on the reefs and, consequently, the processes of formation of the reefs themselves and the sediments surrounding them, are directly functionally related to the production processes in the coral communities (Goreau et al., 1972). Therefore, the study of the regularities of functioning and the production processes of coral biogeocenoses provide the necessary basis for the creation of the theory of growth of the reefs as the facies of sedimentary rock of the earth's crust.

2.1 Reef-Building Organisms

A coral reef is a limestone structure capable of resisting wave action, formed of hermatypic organisms on shallow platforms in the tropical oceans and seas. A variety of benthic fauna and flora occupies the limestone structures and accompanying porous limestone sediment of corallogenic origin. The hermatypic organisms are both animals and plants. Animal hermatypes include the reef-forming corals and certain mollusks (Vermetidae, Tridacnidae). In most reef builders, the active deposition of the carbonates of calcium and magnesium is functionally related to photosynthesis; hermatypic corals, as well as Tridacnidae, carry many symbiotic algae, capable of photosynthesis, within their tissues. Hermatypic plants in coral communities include the red and green algae. Other groups with calcareous skeletons play a significant role in the formation of the reef material: calcareous sponges, sea urchins, polychaetes, ostracods, mollusks and foraminifera.

Usually 30-50 species of madrepore corals inhabit a coral reef, primarily members of the families Agaricidae, Pocilloporidae, Acroporidae, Poritidae, Faviidae, Asterocoenidae, Meandrinidae, Mussidae, as well as hydrocorals (family Milleporidae) and octocorals (family Helioporidae). The plant hermatypes on reefs are represented by 30-40 species of calcareous algae: red (*Lithotamnium*, *Peyssonellia*, *Porolithon*, *Goniolithon*. *Corallina*. *Lithophyllum*, *Sporolithon*, *Tenarea*) and green algae (*Halimeda*, *Penicillus*, *Udotea*). The coral reef includes a rocky calcareous structure and loose limestone sediment. The process of formation of the rocky reef structure includes two successive stages, performed by different species of hermatypes. First, the massive corals (*Favia*, *Siderastrea*, *Hydropora*) or corals with massive, strong appendages (*Porites*, *Acropora*, *Pocillopora*) create the basic skeleton of the growing portion of the reef. Certain calcareous algae also participate in this process, forming massive outgrowths (*Lithotamnium*, *Porolithon*), which, however, play a secondary role (Goreau, Goreau, 1973).

The second phase in the formation of the rocky structure of the reef consists of cementation of its skeletal basis and transformation into a continuous, monolithic structure. This function is primarily performed by the red calcareous algae (*Lithotamnium*, *Porolithon*, *Peysonellia*), as well as the foraminifera, calcareous sponges (*Astrasclera*), mollusks (*Tridacna*, Vermetidae) and polychaetes (Sabellidae).

The calcareous algae are characterized by high rates of growth and metabolism. The rate of formation of lime in these plants is much higher than in corals. Therefore, it is these plants which form most of the carbonaceous rock of the reef. The living corals usually cover only a small portion of the rocky surface of the reef: not over 30-50% in zones of active growth, and less than 5% on the reef plateau (reef flat), occupying most of its surface. The loose calcareous sediment (coral sand) covers most of the surface of the bottom of the lagoon. The red *Amphirhoa*, *Corallina*, *Goniolithon*) and green (*Halimeda*) calcareous algae are most significant in its formation. The *Halimeda* is one of the primary agents involved in the formation of the lime material of the bottom sediments in the reefs of the West Atlantic (Goreau, Goreau, 1973). Another important source of material for the formation of coral sand is the skeletons of dead corals, sea stars, sea urchins, the shells of benthic mollusks, as well as the shells of ostracods, foraminifera and pteropods, ground up by the surf.

2.2 Types of Coral Reefs, their Zonality, Growth and Population with Flora and Fauna

Large reef structures can be subdivided into coastal, barrier and atoll-type reefs. There are transitional forms between these basic types as well. The development of any given type of reef depends on the nature and tectonic mobility of the bottom on which it develops, as well as the intensity of the arrival of terrigenous material from the land. An important factor influencing the formation of the outlines of reef structures is the fact that a most active growth of the corals creating the skeletal basis of the reef occurs on the outer side of the reef, the side directed toward the ocean. It is here that the optimal conditions are created for the growth of coral (Yonge, 1963). On the inside of the reef, the conditions are much worse for the growth of coral; they frequently die here. This factor leads to the formation of circular atoll reefs where the growth of the corals is not limited by a shoreline.

Coastal, or fringing, reefs are usually formed on rocky plateaus of small islands, with no significant terrigenous runoff, not subject to constant tectonic downwarding. One characteristic feature of this type of reef is that there is no lagoon. The reef plateau (reef flat) is directly adjacent to the shoreline. An example of this type of reef is the reef associated with the island of Titia (Fiji) (Fig. 1).

Barrier reefs are also formed on shallow coastline plateaus. They differ from surrounding reefs in that there is a lagoon between the reef flat and the shoreline. The lagoon is formed as a result of the death of corals and cessation of their subsequent growth near the shore. The growth of corals near the shore is depressed by the terrigenous runoff and the decrease of the water in circulation. An example of a barrier reef is the reef associated with the island of Tuvuta (Fiji) (Fig. 2). The structures of barrier reefs achieve gigantic dimensions. The largest of these is the Great Barrier Reef along the east coast of Australia. It is an entire system of reefs extending about 2000 km in length, with a total area of some 250,000 km^2. In contrast to most other reefs, where the main mass of the lime material is created by calcareous algae, the Great Barrier Reef was constructed by corals, the algae being of secondary significance. The thickness of the reef limestone, according to drilling information, is 300-700 m (Ladd, 1969). The second largest barrier reef, over 700 km in length, is located off the north and northeast coasts of the island of New Caledonia. The third is considered to be the barrier reef off the north coast of the Fiji Islands. Its length reaches 400 km. The barrier off the coast of Arabia in the Red Sea is also worthy of mention in any discussion of large barrier reefs.

The circular reefs of atolls develop on the peaks of submerged mountains or guyots, rising nearly to the surface of the water. The growth of the reef in this case is not limited in space, and its circular form is a result of the more favorable conditions for the growth of coral on the outside of the reef. Inside the reef is a sandy lagoon with the residue of a broken rocky base, on which sandy islands usually develop, or underwater pinnacle banks. Inside the lagoon, around the islands and on the remainder of the reef flat, the coral organisms develop in groups, forming so-called "spot reefs."

The structure of a circular reef is shown in Fig. 3, where we see the plan and cross section of the reef of Conflict Atoll (New Guinea). The structure of this atoll reef is similar to that of the barrier reef, except that there are no large islands within the lagoons of the atoll. The largest atolls are Kwajalein Atoll (Marshall Islands) and Suvadiva (Maldive Islands). Their areas approach 2500 km^2.

The zonality of the structure of the reefs has been studied in detail by T. Goreau. The plan which he has suggested rather completely reflects the zonality of the distribution of the primary biotopes as well. The zones distinguished by T. Goreau and his colleagues (Goreau et al., 1972; Goreau, Goreau, 1973) are shown in the cross sections of the primary types of reefs (see Figs. 1-3). They are most completely represented in the barrier reef, so we shall use this plan to present our detailed description of the individual zones and their corresponding biotopes.

The I (inshore) zone is the shore zone, depth less than 1 m. This is the littoral beach. Its population is exposed to the influence of drying out during low tides and to the terrigenous runoffs from the land, leading to silting of the bottom. If silting is severe, mangroves develop in the inshore zone (see III. 1).

Frequently, the inshore zone consists of rocky beds--crust rock or the remainders of an old reef, broken up with cracks. Here we find a rich fauna of mollusks (the gastropods *Tectarius*, *Littorina*, *Nerita*, *Thais*, *Vasum*, *Conus*, *Cymatium*, *Purperita*, *Cypraea*, *Columbella*, chitons), hermit crabs (*Coenobita*, Paguridae), crabs, sea urchins (*Diadema*, *Echinometra*, *Eucidaris*) and the Ophiuroidea (*Macrophiothrix*).

The main source of nutrition of the fauna is the plant fouling of the rocks (periphytons) and plant material thrown out on the beach by the waves. The biomass of the fauna sometimes is quite significant. For example, off the coast of Florida, the biomass of chitons alone in the inshore zone of the reef at the water line is as great as 40 g/m^2 (Glynn, 1973).

The L (lagoon) zone, depth 2-20 m is present in all barrier reefs and atolls. The lagoons of barrier reefs usually are subjected to the influence of terrigenous runoff and differ from the lagoons of atolls in their more eutrophic conditions the predominance in them of heterotrophic processes. The bottom of the lagoon of a barrier reef is frequently silted. Silting of the lagoon greatly influences the composition of its fauna (Goreau, Yonge, 1968). Upon silting, and under

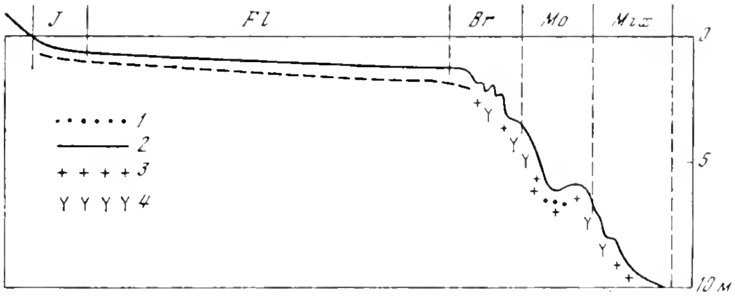


Fig. 1. Diagram of profile and zonality of fringing reef of the Titia Island (Fiji). 1, Sand; 2, Rocky reefflat; 3, Dead coral and fragmentary material; 4, Living coral. For symbols of zones, see text (Sorokin, 1975).

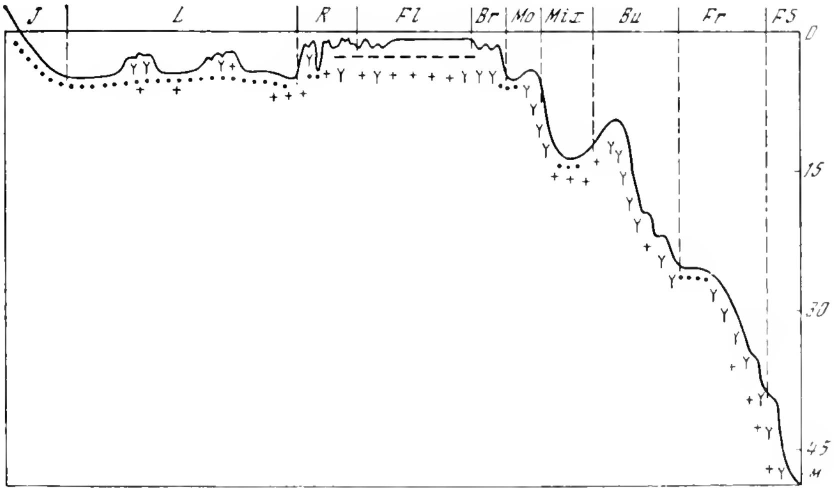


Fig. 2. Diagram of profile and zonality of barrier reef at the Tuvuta Island (Fiji) (Sorokin, 1975). Symbols same as Fig. 1.

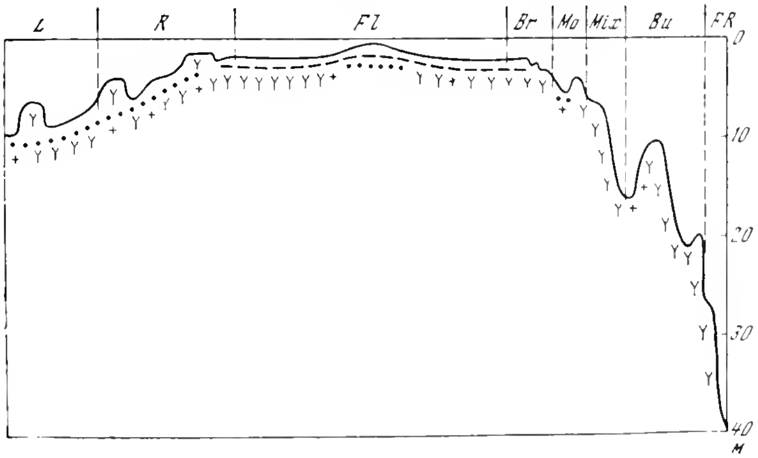


Fig. 3. Diagram of profile and zonality of upwind reef of the Conflict Atoll (Louisiad Archipelago, New Guinea) (Sorokin, 1975). Symbols same as Fig. 1.

the influence of pollution, reduced sediments may appear in the lagoon, containing sulfides and hydrogen sulfide (Sorokin, 1971b). The bottom of the lagoon in atolls is covered with coral sand. If the movement of the water is low, it is inhabited by macrophytes (*Zostera*, *Thalassia*, *Halophila*, *Halodule*, *Syringodium*, *Enhalus*) and psammophilic green calcareous algae (*Halimeda*, *Amphirhoa*, *Avrainvillea*). The sand on the bottom of the lagoon also contains a rich microflora and phytobenthos. They form the diet of the gastropod fauna living here (*Strombus*, *Terebra*, *Cymatium*, Cerithiidae, *Leucozonia*, *Oceanebra*, *Astraea*, *Conus*, *Mitra*, *Oliva*, *Morula*, *Hyalina*, *Tegula*, Turridae). Among the psammophilic fauna, the *Ascidia*, Echinodermata (the sea stars *Linckia*, *Culcita*, the urchins *Diadema* and particularly the *Stichopus*, *Holothuria* and *Ophiodesma*). The *Holothuria* sometimes form massive accumulations, in which their biomass per m^2 of bottom surface reaches 1 kg or more. These accumulations are formed, e.g., by *Ophiodesma spectabilis* in the lagoon of Oahu Island (over 10 indiv./m^2, biomass about 3 kg/m^2) or *Holothuria difficilis* in the lagoon of Eniwetak Atoll (over 100 indiv./m^2, biomass about 10 kg/m^2) (Bakus, 1973, and our own observations). The sand of the lagoon is inhabited by a mass of polychaetes (*Heteroptera*, Sabellidae), as well as varied myobenthos (foraminifera, ostracods, micromollusks) and microbenthos (microphytobenthos and bacteria). An abundant population of the sandy soils of the lagoon gives them high trophic value. The fauna and detritus which can be extracted from the sand form the diet of many benthophagous fish.

Among the corals in the lagoon there are almost always forms which prefer higher levels of illumination (*Porites*, *Oculina*, *Favia*, *Siderastrea*, *Montipora*, *Pavona*, branched forms of *Acropora* and *Millepora*). Conditions for growth of corals in lagoons are frequently unfavorable due to significant water turbidity and a low rate of water exchange. If this is the case, a mass of dead coral and fragmentary material accumulates on the floor of the lagoon. The living coral grows in the lagoon in certain areas, forming "patch reefs," which rise over the bottom of the lagoon in the forms of hills or ridges covered with living coral and corallines.

The R (rear) zone is situated at the internal edge of the reef, depth 1-3 m. This is the rear slope of the reef plateau. It is usually covered with rubble carried down from the reef flat, and is crossed by a network of channels, the bottom of which is covered with sand and clastic materials. Zone R is characterized by significant turbulence from surf waves, which roll over the edges of the reef, as well as tidal currents, and also by a high level of illumination. This creates an optimal condition for the growth of corals, calcareous algae and macrophytes, which inhabit the remainders of the plateau and form independent, broad colonies. The dominant species of corals here are usually the branching forms (*Porites compressa*, *Acropora*, *Seriatopora*, *Millepora*), as well as the fan-shaped and massive forms (*Diploria*, *Montrastrea*, *Favia*, *Favites*, *Hydropora*, *Dichocoenia*, *Acropora cuneata*, *Montipora*, *Porites lobata*, *P. lutea*, *P. asteroides*). On the bottom of the channels between the patch reefs and beneath the lip of the plateau, we frequently see the solitary corals, *Fungia*. Soft corals (Alcyonaria), macroalgae (*Chlorodesmium*, *Thalassia*, *Padina*, *Sargassum*, Turbinaria) and calcareous algae (Porolithon, Jania, Caulerpa) occupy a significant position on the reefs.

The R zone, as a rule, is inhabited by a varied benthic fauna. According to averaged data (Glynn, 1973) on the reefs in the Caribbean Sea in this zone the wet, lime-free biomass of animal matter of the benthos is about 4 kg/m^2 (Table 3). If we include the skeletal mass, the biomass reaches 120 kg/m^2 (Colikov et al., 1972). This is near the maximum possible biomass of the benthos in eutrophic biotopes.

Table 3. Mean biomass of benthic fauna and flora on reefs of the Caribbean basin in the R zone with predominance of the coral Porites (Glynn, 1973).

Group of organisms	Dry matter, including skeletons	Wet biomass of living matter
Madreporaria	12,022	2,855
Echinodermata	263	526
Foraminifera	136	18
Mollusca	59	100
Crustacea	40	149
Sponges	12	58
Polychaeta	7	32
Fish	6	36
Zoantharia and colonial sea anemones	1	4
Zoobenthos, total	12,546	3,780
including filter feeders	-	3,000
Massive macroalgae	1,022	325

The fauna, in addition to coral, includes hydroids (Pennaria). The gastropods are numerous here, inhabiting the loose sediment between reefs. These include primarily the same genera as are found in the sandy lagoons, plus some others (Terebra, Cerithium, Rhinoclavis, Pterygia). Among the large gastropods which inhabit the clastic material and feed on the periphyton, Lambis, Strombus and Cassis predominate. On hard surfaces and in clefts in the reef we find Fissurella, Astraea, Murex, Turbo, Cypraea, Trochus, Lunella, Bursa, Ctena, Chione, Diplodonta, Anodontia), sponges (Tethya), Ascidia, crabs, pencil sea urchins (Cidaridae), Ophiuroidea, starfishes (Culcita), Holothuria (Holothuria, Stichopus), Polychaeta (Serpulidae, Dendrostoma). As to biomass and variety, the benthic population of this zone is among the richest biotopes on the reef.

The Fl (reef flat) zone is the rocky plateau of the reef, depth 0.5-1 m. The shallow reef flat may extend for up to 100 m or more. It is subjected to strong surf action. Individual shoal sections of the reef flat and the limestone rocks located on their surface (so-called "niggerheads") extend above the water surface at low tide. The flat is cut through by channels and cracks, through which the loose bottom sediments and clastic material is transported. The flat is a zone of active calcification. In most reefs, the primary role in this calcification process is played by the calcareous algae (*Neogoniolithon*, *Porolithon*, *Lithotamnium*). In some reefs, they construct a purely algal limestone reef flat (Kornicker, Boyd, 1962; Glynn, 1973). The growth of the limestone mass of the reef flat is accomplished by the algae and also by polychaetes (Dendrostomidae, Sabellidae), which construct the limestone tubules. The entire porous surface of the reef flat is covered with a dense cover of periphyton, consisting of filamentous macrophytes, filamentous blue-green algae and diatoms. Stands of macrophytes with short, strong thalli are also seen (*Turbinaria*, *Laurencia*, *Chnoospora*, *Hydroclarthus*, *Sargassum*, *Padina*), plus large colonies of soft corals (*Zoantus*), colonial sea anemones (*Palythoa*), various individual sea anemones, *Ascidia* and sponges. Living coral (*Acropora*, *Siderastrea*, *Pocillopora*, *Montastrea*, *Diploria*, *Millepora*, *Favia*, *Coeloria*, *Dicoenia*, *Leptastrea*) grow on the surface of the reef flat sparsely in the form of massive crusts or low colonies. The rocky plateau and the "niggerheads" are populated by Gastropoda (*Littorina*, *Nerita*, *Trochus*, *Conus*, *Monetaria*, *Cypraea*, *Murex*, *Bursa*, *Turbo*, *Lunella*, *Astraea*, *Haliotis*, *Mancinella*), various crabs, stars, Ophiuroidea, Polychaeta (Capitellidae, Nereidae, Phyllodocidae). The periphyton and rich fauna serve as food for many fish which come to feed on the reef flat during high tide.

The Br (breaker) zone is the frontal edge of the reef where the waves break, 1-2 m deep. The population of corals living here is constantly subjected to the powerful mechanical effects of the surf. Their growth is determined by their strength. If the reef is in the path of tropical cyclones, the tremendous waves which arise during these storms may crush off all living coral on the outer edge of the reef down to a depth of 5-8 m (Goreau, 1959; Glynn, 1973; Stoddart, 1974). The underlying zones (Mix, But, Fr), after the cyclone passes, are buried in fragments and colonies of broken coral (personal observation of the author on the Lau Islands). Strong typhoons sometimes break down even the rocky reef plateau or bury it in clastic material, as a result of which new islands arise. This occurred at Funafurti Atoll (Ellis Islands) in 1971.

In spite of the strong mechanical action of the surf, conditions for the growth of coral here are optimal, due to the high turbulence and good illumination. Therefore, a dense population of young coral usually arises in the breaker zone, with strong, massive colonies withstanding the waves. Such are the colonies of coral *Acropora* (*Acropora palmata*, *A. cuneata*, *A. corumbosa*), as well as *Stylophora pistillata*, *Millepora platyphilla*, *M. complanata*, *Montipora hoffmeisteri*, *Porites lutea*, *P. asteroides*, *Pocillopora damicornis*, *Diploria strigosa*, and *Favia fragum*. The calcareous algae *Lithothamnium* and *Porolithon*, which form massive colonies in the breaker zone, are very significant in strengthening this zone. Among the benthic fauna, forms which live in cracks in the rocky base and in the colonies of dead corals are predominantly ascidians, sponges, crabs, and various polychaetes.

Mo (moat) zone--3-5 m deep. This zone has the shape of a long moat, along the edge of the breaker zone. The moat is formed as a result of suppression of the growth of corals in the area where the loose sediment and clastic material, carried away from the reef flat by the surf and tide, drifts down. Since active growth of coral proceeds lower down the slope, in the Mix zone, a moat is formed between the Br and Mix zones. Its bottom is covered with sand and a mass of fragments of coral, among which are living solitary corals/*Fungia*. The clastic material is densely populated with periphyton, which is eaten by the large mollusks (*Lambis*, *Bursa*, *Murex*, *Turbo*, *Trochus*).

The main mass of the macrobenthos consists of infauna, which inhabits the colonies and large lumps of dead corals accumulated on the bottom. Here are masses of polychaetes, decapods, amphipods, isopods, oligochaetes, sipunculides and Ophiuroidea.

The Mix (mixed) zone, 4-8 m deep. It occupies the slope, with rather abundant growth of corals, which extend to the next zone.

The Bu (buttress) zone, 8-20 m deep. This is one of the most important and rapidly growing elements of the reef. Here the most intensive growth of corals occurs and the greatest taxonomic variety is seen (Table 4). The growth of corals occurs in strips, located perpendicular to the edge of the reef. It is divided by slots, through which the sediment and clastic material move. As a result of this localization of the active growth of coral, rows of large, limestone humps are formed. Their surfaces are densely covered with corals, which

Table 4. Distribution of massive species of coral over an area of 90 m^2 in the main zones of the frontal part of reef at Heron Island, Great Barrier Reef (Grassle, 1073).

Zone	Species	Total area of colonies, $cm^2 \cdot 10^3$ in an area of 90 m^2
Fl	*Acropora cuneata*	14.0
	A. squamosa	9.7
	Porites andrewsi	3.4
	Pocillopora damicornis	2.6
Br	*Acropora corumbosa*	5.5
	A. cuneata	4.5
	Millepora platyphylla	1.6
	Pocillopora damicornis	1.4
Mix + FR	*Acropora formosa*	196.9
	Montipora sp.	65.7
	Acropora hyacinthus	36.1
	Seriatopora hystrix	5.3
	Pocillopora damicornis	2.2

find optimal conditions here for their growth: a high degree of water turbulence, sufficient illumination, intensive development of plankton, consuming the organic matter which flows down from the reef. The large fan-shaped and branched forms of coral predominate: *Agaricia*, *Mussa*, *Favia*, *Acropora*, *Seriatopora*, *Madracis*, *Pterogorgia*, *Gorgonaria* bloom (*Ellisella*, *Nicella*, *Viminella*, *Pseudopterogorgia*, *Plexaura*) along with soft corals (*Sclerophytum*), which compete with the corals for the solid substrate and frequently form continuous growths. The Bu zone is rich in sponges (*Ircina*, *Mycale*, *Agelas*, *Verongia*), some of which reach almost 1 meter in diameter. The fauna includes crinoids (*Nemataster*), boring sponges (*Clionidae*) and mollusks (*Lithophaga*, *Fungiclava*), which make paths through the living coral. An unusually rich fauna inhabits the dead colonies of coral and the rocky base. In one such colony, brought up from a depth of 15 m, some 8000 individual organisms of macrobenthos of 50 species were found (McCloskey, 1970).

The FR (fore-reef) zone, depth 20-40 m. This zone occupies a steep slope, on which a kind of cliff (so-called "sill-reef") is sometimes forming, which consists primarily of the massive corals *Montastrea*, *Agaricia* and *Madracis*. This zone is characterized by a rapid growth of corals, which form a large colony (*Astrangia*, *Agaricia*, *Montipora*, *Millepora*, *Mussa*). Calcareous algae (*Halimeda*, *Peyssonellia*) develop intensively here as well as a rich zoobenthos, which includes various attached forms (polychaetes, sea lilies, Bryozoa, hydroids, gorgonarians, ascidians, colonial sea anemones, soft corals). A significant role in the deposition of lime in this zone is played by the calcareous sponges (Sclerospongia), which reach a significant size and are encountered in large quantity, particularly on the walls of the canyons and caverns (Goreau, Goreau, 1973).

The discovery of the abundant development of coral communities at significant depths at the foot of a reef (Goreau, 1959) was one of the most important achievements of Goreau in the study of coral ecosystems. His observations on the structure of the deep zones of the various reefs have shown that the structural form of the reef is determined not by processes of erosion, but by the localization of the growth of corals. The localization of the coral growth, in turn, is regulated to a significant extent by the complex movement of the bottom sediment and clastic material over the profile of the reef, since in sediment covered areas of the reef, over which it flows, colonies of massive corals cannot settle and develop, creating the buttresses of the reef. Their surface can be inhabited only by solitary corals (*Fungia*), which lie freely on the ground, or by highly branched forms (certain Acropora). As the corals grow, the troughs filled with reef sediment are converted into deep canyons with steep walls. These canyons are gradually covered over by massive colonies of coral growing on their side walls, and converted into caverns. In the Br, Mix and Bu zones, caverns are normal elements of the external side of a reef.

Individual species of organisms are rather clearly restricted to specific zones of the reef. However, if we analyze the species composition of the madrepore corals and algae in various zones of the Jamaica and Great Barrier Reefs (Goreau, Goreau, 1973; Grassle, 1973), we can see that certain species of coral inhabit all zones of the reef. These opportunistic" species include, for example, Pocillopora damicornis, Porites asteroides, Montrastrea annularis, Acropora cervicornis, Stylopora pistillata. There are species (e.g., Porites porites) which populate the shoals (zones L and R) and the deeper zones of the outer slope (Bu, FR), but are practically absent in the surf zones on the rocky plateau (Fl, Br, Mo, Mix). Finally, a number of species occupy the slope biotopes (Bu, FR, FRS) but are not encountered at depths of less than 20 m (Agaricia grahami, Madracis mirabilis, Mycetophylla reesi, Acropora hyacinthus, Seriatopora hystrix). The "opportunistic" forms, encountered in all zones of the reef, characteristically are able to change the form of their colonies, depending on conditions of illumination and turbulence: branched colonies in the lagoon, and massive colonies on the reef flat.

2.3 Ecological and Physiological Features of Reef-Forming Corals and Factors Influencing their Growth and Distribution

Many fundamental peculiarities of the coral communities result from the ecological-physiological properties of the hermatypic corals themselves. They include: the diversity of ways of feeding of corals, including photosynthesis, the coupling of the process of calcification with photosynthesis and the antagonistic interactions between some coral species.

The diversity of ways of feeding of madrepore corals makes them, in a certain sense, a unique set of hydrobionts. They possess practically all known types of feeding behavior peculiar to aquatic invertebrates and have the specific morphologic structures and enzyme mechanisms for this purpose. Because of the presence of symbiotic algae in the tissues of their polyps they are capable of autotrophic nutrition, like green plants. Their growth, like the growth of plants, depends on light also because the precipitation of $CaCO_3$ and $MgCO_3$ from the water by them is directly dependent upon illumination (Muscatine, Cernichiari, 1969; Goreau, 1963; D. J. Barnes, 1973). The well-developed ciliar epithelium and the streamlike movement of mucus along the tentacles of the polyps allow the corals to obtain nutrition from the detritus and microorganisms suspended in the water. The operation of the ciliate apparatus and the presence of the required enzymes gives them the ability to utilize organic matter dissolved in the water. Finally, the polyps are capable of predatory feeding. The polyps catch their prey using their stinging cells, then digest the prey inside their gastral cavity or outside of the polyp's body by means of their mesenterial filaments. These combined ways of feeding eliminate the basic factor which limits the development of life in the poor surface tropical waters of the ocean: the shortage of nutrients such as nitrogen and phosphorus. Actually, due to their heterotrophic nutrition, the corals can utilize the organic sources of nutrients (Sorokin, 1973a). The processes of autotrophic production and heterotrophic decomposition of organic matter, combined in a single organism, provide a closed cycle of nutrients with minimum losses into the environment (Johannes et al., 1970). This is not feasible for heterotrophs, the metabolism of which occurs only under conditions including liberation of nitrogen (in the form of urea) and phosphorus (in the form of inorganic phosphate) into the environment. These products of heterotrophic metabolism are utilized in the autotrophic biosynthesis of the zooxanthellae, without leaving the organism of the polyps. It has been established that hermatypic corals, having zooxanthellae, excrete much less inorganic phosphate per unit of biomass as compared with hermatypes, which do not have zooxanthellae, or with other marine animals (Yonge, Nicholls, 1931; Pomeroy et al., 1974).

An intensive photosynthesis (Table 5) is inherent for the corals, in spite of the fact that the biomass of the zooxanthellae represents only a few percent of the biomass of the polyps (Table 6). The mean intensity of photosynthesis of madrepore corals is 0.2-0.3 mg C/g of dry matter of the colony, or about 5 mg C/g of organic matter of the polyps per day. The production of photosynthesis usually exceeds the losses of polyps to metabolism by 1.5-3. Therefore, for most corals inhabiting areas with optimal conditions of illumination, energy losses can be completely compensated for by photosynthesis. When this occurs, about half of the organic matter synthesized by the zooxanthellae is found within a few hours as part of the tissue of the polyps (Muscatine, 1967, 1973; Von Holt, Von Holt, 1968). Such an intensive autotrophic production of organic matter is achieved due to a high intensity of photosynthesis of the zooxanthellae, the daily P/B coefficient of which is about 2 to 5.

In addition to the production of organic matter, the functioning of the zooxanthellae enhances the process of calcification in the construction of the skeleton of hermatypic corals, and so of the growth of the reef itself. With the use of isotope Ca^{45} it has been shown that the process of accumulation of calcite in the skeleton of the corals depends directly upon the intensity of the light and the presence of zooxanthellae (Goreau, Goreau, 1960). The addition of specific photosynthesis inhibitors to the water inhibits also the process of precipitation of calcium carbonate in the skeleton of the corals.

The capability of corals to feed on microplankton has been proven experimentally, using phytoplankton and bacteria labeled with C^{14} or S^{35} (DiSalvo, 1973; Sorokin, 1973e). This sedimentation mode of feeding of corals is based on trapping of the nutritious particles (bacteria, algae, protozoa) by the mucous surface of the body of the polyp and their transfer by the action of cilia to the mouth (Yonge, 1968; Muscatine, 1973). Apparently, the coenosarc (the tissues covering the surface of a colony between polyps) also may participate in the process of sedimentation feeding, which may significantly increase the intensity of sedimentation feeding (Goreau, 1959). According to the observations of Goreau, the nutritious particles which precipitate onto the mucous surface are transferred toward the polyps by the movement of the mucus.

Determinations of the intensity of the sedimentation way of heterotrophic feeding of massive species of coral (Pocillopora, Porites, Fungia, Montipora), using bacteria labeled with C^{14} as the food, have shown that this method of nutrition can compensate for up to 10% of the daily losses in metabolism (Fig. 4). The phytoplankton is consumed and assimilated by the polyps much more poorly than the bacteria, since the polyps are not capable of digesting plant cells (Yonge, 1930).

Table 5. Intensity of photosynthesis and respiration (μg C/g dry weight per day) in various elements of the benthic communities of coral biocenoses (Sorokin, 1973e, 1975a).

Reef zone	Object and its status: ℓ - living coral; d - dead coral, covered with periphyton	Organic matter, %	Photosynthesis P	Respiration D	P:D	$P:C_{org}$, %
R	Coral Pocillopora caespitosa (ℓ)	1.15	305	306	1.0	4.8
Fl	Coral Pocillopora sp. (ℓ)	1.52	227	196	1.4	2.7
Fl	" " " (d)	2.80	3.2	247	1.3	2.0
R	Coral Montipora verrucosa (ℓ)	6.27	190	170	1.1	0.6
R	" " " (d)	5.41	270	360	0.8	0.9
R	Coral Acropora sp. (ℓ)	1.10	296	207	1.5	5.1
R	" " " (d)	2.18	182	98	1.8	1.5
R	Clastic material from dead coral	1.49	283	110	2.5	3.2
L	Coral sand	1.10	58	50	1.2	1.0
R	" "	1.50	37	26	1.4	0.4
Fl	Lump of naked reef flat stripped off by a typhoon action.	2.30	290	218	1.3	2.3
Fl	"Regenerative" sediment, washed from dead colonies of coral	2.10	550	1220	0.2	4.8

Table 6. Indices of biomass and metabolism of two species of the coral Pocillopora (Sorokin, 1975).

Species of coral	Point of collection	Organic matter in colony, % of dry weight	Biomass in C_{org}							Metabolism				
			Zooxanthellae			Polyps				Photosynthesis P		Respiration D		
			No. in one polyp	µg C in one polyp	% of C_{org} in one polyp	µg/1 g dry matter	µg C/indiv.	% of total C_{org} of colony	C_{org} % of dry weight of colony	µg C/g/day	P/B_z	µg C/g/day	P:D	D/B_p, %
P. damicornis	Calvados atoll, New Guinea	1.46	2050	0.51	2.1	110	24	34	2.64	325	5.8	270	1.20	10
P. caespitosa	Scott Reef, eastern Indian Ocean	1.25	2400	0.42	2.2	170	19	48	3.23	320	4.5	490	0.62	15
P. caespitosa	Funafuti atoll, Ellis Island	0.15	1900	0.26	1.7	260	15	61	3.90	305	4.5	306	1.00	8

Note. B_z and B_p are the biomass of zooxanthellae and polyps, µg C/g of colony's dry weight.

In evaluating a relatively low rate of sedimentation and predatory feeding by coral (Johannes et al., 1970), we must consider that coral receives the bulk of the energetic material it needs by photosynthesis of zooxanthellae. The heterotrophic feeding serves corals not only as a source of energy, but also as a way of supplying them with necessary nutrient salts, vitamins, trace elements, as well as with some essential amino acids which are not produced by the zooxanthellae.

The digestive organs used for predatory feeding are the mesenterial filaments which line the edges of the septa in the intestinal cavity. These filaments are mobile and may extend outside the oral aperture by a distance of up to 10 cm, causing predigestion of large prey items outside the intestinal cavity. They literally weave around the food and digest it with exoenzymes.

Experiments have demonstrated that when there is a significant concentration of zooplankton, corals with large polyps (such as Montastrea) are capable of completely satisfying their requirements for food by predatory feeding (Coles, 1969; Porter, 1974). However, usually, the concentration of zooplankton over reefs is so low that it cannot satisfy the energy demands of the coral (Johannes et al., 1970; Johannes, 1974). Predatory feeding of coral is probably increased during the period of massive development of invertebrate larvae (veligers, trochophores, echiniopluteus larvae, etc.). Calculations of the difference in concentration of plankton in the lagoon and in the surrounding atoll waters have shown that the consumption of plankton by the coral community can cover about 5-10% of the energy expended in metabolism (Johannes et al., 1970; Glynn, 1973).

Furthermore, coral is capable of feeding effectively on organic matter dissolved in the water at concentrations near the natural concentration: 1-2 mg c/ℓ (Stephens, 1960). With this concentration glucose or protein hydrolysate, the corals in our experiments assimilated the dissolved organic matter in quantities sufficient to cover 15% of the daily expenditure for metabolism (Sorokin, 1973a). About half of the labeled organic matter consumed by the coral is included in the composition of the matter of the polyps (Lewis, Smith, 1971).

Experiments on Pocillopora have shown that the rate of consumption of one labeled amino acid at a concentration of 0.1 mg C/ℓ is not reduced when other nonlabeled amino acids are added at 100 times greater concentration (Sorokin, 1977). Obviously, the corals have a mechanism for enzymatic (permease) transport of dissolved organic matter into their cells. Effective consumption of organic matter is provided by the large surface area in contact with the water due to the ciliated epithelium and mesenterial filaments. The significance of this way of feeding of corals under natural conditions requires further clarification.

The phenomenon of interspecific antagonism and aggressiveness of coral species has considerable value in the population ecology of coral communities (Lang, 1973). An entire hierarchy of such relationships has been found between various species of coral. When two species of

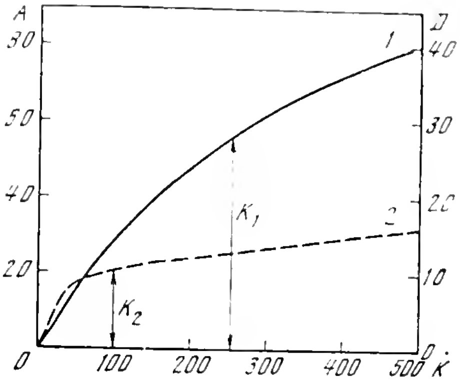


Fig. 4. Intensity of assimilation (A, μg C/g •day) of food labeled with C^{14} by coral with various food concentrations (K, μg C/liter): 1, Dissolved organic matter (algae protein hydrolysate); 2, Bacterial plankton; D, assimilated food, % of expenditure for metabolism (with correction for loss of C^{14} during time of experiment); K_1 and K_2--probable natural concentrations of bacteria and dissolved organic matter in the water around the coral reefs.

coral come in contact, the polyps of the more aggressive ("stronger") species extend their mesenterial filaments toward the "weaker" species, enclose and digest its polyps. Most aggressive are the massive, slowly growing species of *Favia*, "weakest" are the species of *Agaricia*, which live at considerable depth and, apparently, do not experience great competition from the other madreporaria. *Acropora* occupy an intermediate position.

The growth rate of hermatypic corals depends to a great extent on the level of illumination at the point of attachment of the colony. In the dark, the hermatypic corals die within a few months. Under optimal growth conditions, in two or three years, coral colonies can grow to a diameter of 10-20 cm, doubling their size each year. The mean age of colonies in the zones of active growth (FL, Br, But) is about 5 years, the maximum age--up to 140 years. The mortality of young colonies is great--20-40% within 3 years (Connell, 1973). In spite of the high rate of growth of young corals, replacement of their populations after passage of a destructive typhoon is quite slow. The additional stage of settlement of the damaged frontal zone with corals and the succession of communities which follows extend over a period of 3-5 years (Stoddart, 1962, 1974; Glynn, 1973), while full restoration requires over 30 years.

The composition and population of corals is significantly influenced by such natural enemies as the boring sponges *Clione* and the mollusks *Ithophaga* (Pang, 1973). They drill holes into the living coral and decrease its resistance to the surf. Many reef animals (sea urchins, sea stars, crabs, polychaeta, gastropoda, fish) feed on the coral, eating the polyps or removing their outer layer. The most dangerous predator for the coral is the starfish *Acanthaster planci*. Over the last 10-15 years, population explosions of this animal on certain reefs in the Indian and Western Pacific Oceans have been observed (Endean, 1973; Connell, 1973). These large--mean diameter 30 cm--stars are usually found quite rarely on the reefs, a few individuals per km^2. Following massive breeding, their population density increases to several individuals per 10 m^2. Moving over the reef in compact groups, they destroy up to 90% of the corals. The coral requires many years to recover after they pass.

2.4 Periphyton, Phytobenthos, Primary Production and Microflora in Reef Biotopes

When we speak of the algoflora of a reef and its production, we generally mean macrophytes and calcareous algae. However, most of the primary production in coral biogeocenoses is created, apparently, not by the macrophytes, but rather by the periphyton and microphytobenthos. The periphyton abundantly overgrows all rocky surfaces of the reef flat, the porosity of the calcareous material of the flat significantly increasing the area and mass of the overgrowth. The periphyton develops particularly intensively on colonies of dead coral and their fragments. Most of the periphyton consists of filamentous and mucous forms of bluegreen algae and diatoms (Osterobium, Calotrix, Microcoleus, Shizotrix, Rivularia, Nitzschia, Navicula, Cymbella). In addition to these, we also see certain macrophytes with short, filamentous thalloms (dwarf forms of Laurencia, Sargassum, Polysiphonia and Gelidella). The biomass of algae in the periphyton is 2-5 mg/g (Sorokin, 1973d). The photosynthesis of the periphyton over the dead corals amounts to 100-500 μg C/g dry weight of dead colony per day (Table 7).

The photosynthesis of the periphyton on dead corals expressed as dry weight of the colony, averages close to that on living coral of the same species and configuration. The daily production of photosynthesis of periphyton over dead corals is about 3% of the total content of organic matter, averaging 3-5 g C/m^2. The production is equally intensive in periphyton over the clastic material and over the reef flat rocks (Tables 5, 7). The production of macrophytes on the Great Barrier Reef averages about 0.3 g C/m^2 per day (Grassle, 1973).

The respiration of the periphytonic community is also rather intensive, 60-100% of the production by its photosynthesis. The same relationship between photosynthesis and respiration was also found for living corals (Tables 5, 6). Thus, the periphyton community, like the living corals, fully supplies itself with energy by photosynthesis, in spite of a significant quantity of heterotrophic organisms in it. It is quite probable that some closed cycles of nutrients exist in the periphyton community, since the primary producers and reducers are combined into single agglomerates by mucus excreted by the algae. This, in particular, may explain the richness of the periphyton, even on the outer side of the reef, which is washed with water that is practically devoid of the inorganic forms of nutrients.

The coral sand which occupies most of the area of the atolls and of certain barrier reefs is also abundantly populated with microscopic algae. The sand particles are fragments of coral skeletons or coralline algae of the shells of foraminifera and ostracods. They are covered with a mucous film containing algae and bacteria. The wet biomass of phytobenthos in the sands, based on the results of direct measurements (Sorokin, 1973d, e), was 0.5-1 mg/g, based on calculations of the intensity of photosynthesis, about 2 mg/g. Measurements of the photosynthesis of the phytobenthos by the radiocarbon and oxygen methods (Sorokin, 1971b, 1973d,e, 1975a) have yielded similar values: 30-60 μg C/g per day. The thickness of the photosynthesis layer in the coral sand on Funafuti Atoll is 3 cm, but it decreases rapidly in the first centimeter of sand. Calculation of the production by photosynthesis of the phytobenthos in the sand yields a value of about 1 g C/m^2, which is 3-5 times higher than the primary production of photosynthesis by phytoplankton in the 100-meter euphotic layer of tropical waters.

Table 7. Biomass and daily production of microflora on coral sand (s) in periphyton over the dead coral (dc) and in periphyton over the rocky reef flat (r) in the Fl zone (Sorokin, 1975a).

Sampling location, condition of reef	Depth, m	Object	Organic matter, %	Total No. of bacteria, 10^9/ g substrate	Biomass of bacteria, μg C/g
The Scott Reef (East Indian Ocean): reef with abundant growth of corals	0.5	s	1.9	4.2	315
		dc	2.6	2.5	180
The Barrier reef at the Bili-Bili Island, Maclay Coast (New Guinea): significant erosion of terrigenous material, abundant coral growth	1	s	1.3	2.2	270
		dc	4.6	3.8	280
The Ngele-Levu Atoll (Fiji): hollow reef flat, almost no living corals, algae predominate	2	s	1.5	0.3	19
		dc	3.4	5.1	630
The Funafuti Atoll (Ellis Island): hollow reef flat corals carried away by typhoon	0.5	r	1.5	2.7	290
The Funafuti Atoll, half-destroyed reef with sparse coral	1	s	0.8	1.2	46
		dc	5.6	2.8	215
Coastal reef in the Kaneohe Bay, Oahu, Hawaii: sparse living coral, mass of zoantharia, polluted area.	1.5	s	5.1	3.6	220
		dc	1.5	1.0	28
		r	3.0	9.7	147

The intensity of respiration of the community of microorganisms populating the coral sands of an unpolluted living reef is, on the average, comparable to the magnitude of photosynthesis (Table 7). Respiration is significantly greater than photosynthesis in the sands deposited directly beneath the living coral, and in the loose sediment of a polluted reef (Sorokin, 1973e). Each day, photosynthesis causes the renewal of about 1% of the total organic carbon in the sand.

The intensity of photosynthesis of the coral community is 3-10 g C/m^2 per day (Sargent, Austin, 1953; Odum, Odum, 1965; Odum et al., 1959; Kohn, Helfrich, 1957; Kinsey, Kinsey, 1967). This is 30-50 times higher than the production of phytoplankton in the column of oligotrophic waters surrounding the reef.

The most important component in the periphytonic communities of the reef is bacteria. Their population is $1\text{-}5 \cdot 10^9$ cl/g in the sand, $3\text{-}6 \cdot 10^9$ in periphyton, and up to $10 \cdot 10^9$ in regenerative sediment (Table 7). Such a high population of bacteria can be found only in the bottom sediments of eutrophic lakes. The number of bacteria in the regenerative sediment of the polluted reef in Kaneohe Bay, Hawaii, was close to the number in the active silt of sewage purification plants (Sorokin, 1973e).

Most of the microflora of the periphytonic overgrowth of solid substrates (dead coral, the rocky reef flat) consist of mobile filamentous flexibacteria such as *Leucotrix*, as well as catenulate bacteria such as *Cladotrix* and *Crenotrix*, which usually develop in bodies of water rich in organic matter.

The biomass of bacteria in the periphyton and in bottom sediments of the coral reefs varies within 50-500 μg C/g, or about 5 g/ℓ of wet biomass (2-3% of the total organic matter of the substrate). The production of microflora in the bottom sediments and periphyton is 20-200 μg C/g per day, the P/B ratio averages 0.2-0.7. Thus, the matter of the benthic microflora of the coral reef is totally renewed in 2-5 days.

2.5 Structure and Productivity of the Planktonic Communities over Coral Reefs

The plankton of reefs is relatively much poorer than the benthos, its biomass and production being many times lower than that of the benthic communities. Thus it mibht be concluded that the plankton is insignificant in the energetics and functioning of the ecosystem of the coral reef. However, this conclusion would be erroneous, because the predominant benthic fauna of the reef are filter-feeders and sediment feeders which consume the plankton (Glynn, 1973). The underevaluation of the significance of the plankton is partially due to a failure to consider the main producing and nutritive component of the plankton in coral communities--the bacterioplankton. The plankton and the organic matter dissolved and suspended are the key links by means of which the individual biotopes of the reef are energetically connected, thus forming the unified coral reef ecosystem. This energetic connection is achieved both by direct transfer of the larval planktonic stages, which serve as a source of nutrition for the coral, and by transfer of dissolved or aggregated organic matter, liberated by the coral and algoflora, detritus, bacteria, algae, protozoa which is washed out into the water from the coral sand, and periphyton of the shallow zones of the reef by the action of the waves and currents.

The wet biomass of phytoplankton over the reef averages 20-100 mg/m^3; the production averages 10-30 mg C/m^3 (Sorokin, 1971c, 1973b). It is significantly higher on reefs located in eutrophic regions, for example, New Guinea or Puerto Rico (Glynn, 1973). The lowest biomass and production of phytoplankton are reported for reefs located in oligotrophic waters of the ocean (Table 8). The seasonal nature of phytoplankton development is of great significance. During periods of maximum development, the biomass and production of phytoplankton may increase by an order of magnitude in comparison to the mean annual values (Sournia, 1969). Periods of massive appearance and precipitation of benthos larvae in the tropics coincided with the period of phytoplankton maximum (Fig. 5).

The phytoplankton is usually dominated by diatoms (Sournia, 1969; Glynn, 1973). According to our observations, the important components of the phytoplankton in the water above reefs are the dynoflagellates of the genus Porocentrum, as well as filamentous blue-green algae, washed out from the periphyton and phytobenthos by the surf. If the blue-green alga, Trichodesmium rubrum is developing in the surrounding waters of the ocean, it appears in a significant quantity in the water above the reef, as well, at times representing as much as 90% of the total phytoplankton biomass.

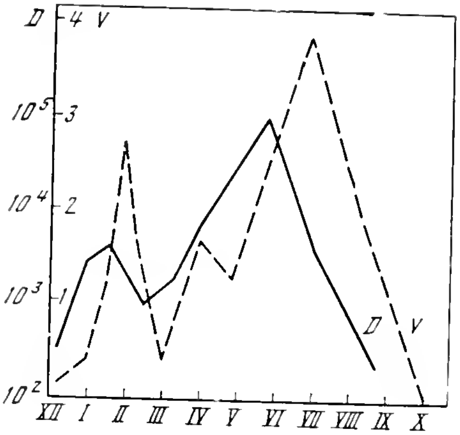
In spite of the intensive water exchange, the distribution of phytoplankton and its production above the reef are usually not uniform: The maximum values are observed above the outer slope of the reef (Br-FR zones), the minimum values in the lagoon. This may be either a result of the consumption of the phytoplankton by the reef fauna (Emery, 1968; Glynn, 1973) or a result of a more intensive breeding of phytoplankton over the outer slope of the reef which is enriched by the runoff of nutrients and biologically active substances from the reef flat.

The primary component of the plankton in the water over the reef in most cases is not phytoplankton, but rather bacterioplankton. The biomass of phytoplankton over reefs usually does not exceed the limits characteristic for oligotrophic waters the biomass of bacterioplankton corresponds to the level of mesotrophic waters, and sometimes of eutrophic waters of the ocean. The biomass of bacteria exceeds the biomass of phytoplankton by an average of 5-10 times, production--by 1.5-2 times. The total population of bacteria in the water above the reef averages $0.5\text{-}1.5 \cdot 10^6$ cl/ml, their biomass--20-80 mg C/m^3 (0.2-0.8 g/m^3 wet mass). In certain cases, the population of bacteria may reach 3 million cl/ml with a biomass of over 130 mg C/m^3. These magnitudes were noted in New Guinea (organic-rich terrigenous runoff) and in the lagoon of the polluted reef of Kaneohe Bay, Oahu, Hawaii (Sorokin, 1973e). Most of the bacterioplankton consisted of rod-shaped forms. About 30% of the cells were joined into aggregates--accumulations 5-15 μm in diameter. Their formation is a result of the property of a part

Table 8. Phytoplankton and microflora in water over coral reefs (Sorokin, 1975a).

Sampling location and description	Reef zone, depth, m	Phytoplankton		Bacterioplankton			
		Biomass (B), μg C/m^3	Production (P), μg C/m^3/day	Number 10^6cl/ml	Biomass (B), μg C/m^3	Production (P), μg C/m^3/day	Destruction rates μg C/m^3/day
Scott reef, Indian Ocean: atoll with rich coral growth	L, 1	10.6	29.3	1.54	116	14.3	41
	Fl,0.5	3.5	9.4	1.29	51	11.8	33
	Bu, 8	2.8	4.6	1.69	146	25.0	71
Barrier reef at Bili-Bili Island (coast of Maclay, New Guinea): rich terrigenous run-off, abundant coral growth	L,1.5	2.9	3.1	3.32	133	27.3	77
	Fl, 1	3.2	7.0	1.39	53	14.0	39
	Bu, 10	8.7	9.4	2.58	123	30.7	86
	L,1.5	1.1	1.5	0.49	5	8.5	24
	FR, 2	1.3	1.7	0.64	20	17.4	49
	FR,30	0.2	0.7	0.16	4	6.9	19

Fig. 5. Seasonal fluctuations in population of diatoms (D, cl/ℓ) and veliger gastropods (V, 10^3 indiv.), settling each month onto an area of 1 m^2 (according to Glynn, 1973).



of the bacterial population, that it forms aggregations in the process of multiplying (Sorokin, 1971a,b, 1973c), rather than a result of the cementing effect of the coral mucus, as was assumed earlier (N.B. Marshall, 1968; Johannes, 1967).

The maximum values of biomass of bacterioplankton are usually noted in the shore zone, where the surf washes the microflora from the bottom sediments, and also in the frontal zone of the reef (Br-FR zones). Here also, we frequently see the greatest value of bacterial production. The values of daily production of bacterioplankton varied within limits of 10-50 mg C/m^3, the daily P/B ratio was 0.2-0.4 in the lagoon and 0.5-2 over the outer slope of the reef. The low values of P/B coefficient in the lagoon, particularly along the shore, are apparently related to the input of a large quantity of benthic microflora, slowing the multiplication rate in the water column.

The information available on the zooplankton of the reef waters is sparse and contradictory (Johannes et al., 1970; Emery, 1968; Glynn, 1973). It is difficult to observe, since most of it hides during the day in the sand and in stands of macrophytes, and appears in the water only at night. Also, the biomass of mesozooplankton on the reefs is subject to great seasonal variation (Fig. 5), since a significant portion of it consists of the meroplanktonic larvae of benthic animals (M. J. Allen, 1957). Data on the biomass and seasonal changes in organisms of the microzooplankton (nauplial stages of copepoda, infusoria) are severely lacking.

The coral communities are inhabited by a rich and varied ichthiofauna. A significant portion consists of benthophages, which feed along with benthic animals also on detritus, algae, periphyton, and also living corals. The biomass of fish in reefs was estimated as 100-300 kg/ha (Glynn, 1973). The planktonophagous fish inhabiting the area around reefs is dominated by juvenile oceanic pelagic species, which find good feeding conditions here.

2.6 Nutrition and Food Connections of Reef Fauna

For many common species of the infauna, and particularly for the corals, a diversity of modes of feeding is characteristic, including symbiotic autotrophy. Among the animals which have plant symbionts in addition to the corals are the actinia Anthopleura, the soft corals Zooanthus, the colonial actinia Palythoa, the gastropod mollusks (Tridachia, Placobranchus), and the bivalve mollusks (Tridacna, Hippopus). The Tridacna, which are quite large (length up to 1 m, weight up to 250 kg), frequently play a significant role in the productivity and accumulation of calcareous material on the reefs.

The symbiotic algae include the dinoflagellates (Zooxanthellae), the green algae (Zoochlorellae) and individual chloroplasts of free-living siphon algae, consumed by their animal hosts (Tridachia). These chloroplasts accumulate and function in special mucous glands of the mollusks (Trench, 1971).

In addition to the ability to use solar energy for autotophic nutrition, most coelenterates (corals, hydroids, actinia) as well as the bivalve mollusks, sponges and Ascidia, are able to effectively utilize dissolved organic matter in sea water (Sorokin, 1973a; Sorokin, Wyshkwarzew, 1972). The consumption of dissolved organic matter begins at a concentration of some tens of µg/ℓ (Fig. 4), whereas the concentration of low-molecular organic matter in the water above a eutrophic coral community is 0.2-1 mg C/ℓ, with the total content in the water of 3-5 mg C/ℓ. Its liberation by the benthic community in the process of photosynthesis could be as high as 0.3-0.6 mg C/ℓ per day (Khaylov, 1971). Consequently, we can assume that the dissolved organic matter of sea water, like the plankton and seston, participates in the transfer of energy between reef biotopes, bonding them into a unified ecosystem.

Another important source of nutrition for benthic filter feeders on the reef is the bacterioplankton. Studies by the radiocarbon method have shown (Sorokin, 1973e; Sorokin, 1973b,c) that among the filter feeders which feed intensively on the bacterioplankton are the sponges, bivalve mollusks, ascidians, polychaetes (serpullides, sabellides), corals, hydroids and zoantharians (Palythoa). The most active consumers of bacterioplankton were found to be the sponges, polychaetes and bivalve mollusks, for which, at a concentration of bacterioplankton near the natural level of around $1\text{-}2 \cdot 10^6$ cl/ml, the filtration rate reaches 600 ℓ/g of organic carbon of the filterers' body per day. The filtration apparatus of these animals is so highly perfected that they can consume bacteria with a biomass of less than 10 mg/m^3--50-100 times lower than the natural concentration of bacterioplankton in the water over a reef and 3-5 times lower than that of the surface waters of the neritic zone of the ocean. Consequently, they can utilize bacterioplankton from the oceanic water passing over the reef and thus include this external source of energy in the metabolism of the reef.

The daily ration of the active filter feeders of the reef, feeding on bacterioplankton at its natural concentration, is 5-50% of their body weight, sufficient to compensate for the expenditures for metabolism. For the sediment feeders (madreporarians, zoantharians, hydroids) and coarse filter feeders, which filter out primarily bacterial aggregates measuring more than 5 µm in diameter, bacterioplankon makes up only a portion of their daily ration. For example, the coral Pocillopora, by feeding on bacterioplankton and dissolved organic matter with a concentration near the natural concentration, can compensate for about 1/4 of the metabolic expenditures. It must be considered that the value of the bacterioplankton for the corals could be more in the nutrients they contain than in the energy which they receive in sufficient quantity from the symbiotic Zooxanthellae.

Phytoplankton, as a source of food for filter feeders, in most cases plays a much less significant role than does bacterioplankton. Its biomass in the water of coral biogeocenoses is usually 5-10 times less than that necessary for the normal nutrition of the reef organisms. Only in the productive zones of the ocean or during periods of the maximum development of phytoplankton in oligotrophic waters can we expect participation of phytoplankton in the nutrition of benthic filter feeders and sediment feeders of the reef to be significant. The question of the value of phytoplankton as a source of food for the coral has not yet been answered. The available data indicate that the madreporarians practically do not consume it and are not capable of digesting the plant cells (Yonge, 1931; Sorokin, 1973a). However, the alcionarians and zoantharians can feed on phytoplankton (Sorokin, 1973e).

We can also suppose the microzooplankton has to be a significant component in the trophic connections of the reef. However, there are no quantitative data available on this question. The mesozooplankton of the reef is consumed both by the corals themselves (Porter, 1974) and by the hydroids, Zoantharia, Actinia, Gorgonaria, Calani and Polychaeta.

Attempts to estimate the food value of net zooplankton for the coral have been made on the reefs off the Bermuda Islands (Johannes et al., 1970). It was found that even with complete consumption of the zooplankton carried above the reef by currents by the coral (Diploria), it could compensate for only about 5% of the expenditure of the coral community for metabolism. However, the biomass of zooplankton on the reefs in eutrophic regions off Florida and the Laccadive Islands is quite high--up to 0.2-0.5 g/m^3 (Emery, 1968; Tranter, A. Jacob, 1969). The meroplankton is also quite numerous, particularly at night.

The food resources created by benthic algoflora and the bacterial population of the sediment and reef periphyton are used by many benthic invertebrates and fish. Many of them take in the bottom sediment nonselectively: coral sand, detritus, regeneration sediment, formed among accumulations of dead colonies of coral (Bakus, 1973). As was shown earlier, the bottom sediments of the reef contain an exceptionally rich microflora and phytobenthos. It is therefore not surprising that even nonselective consumption is energetically expedient for animals. Experiments using C^{14} have shown that the Holothurioidea Ophiodesma and Gastropoda Nerita digest the microflora contained in the sediment and can fully satisfy their nutient requirements with it alone (Sorokin, 1973e). The quantity of bottom soil consumed per day by these animals frequently exceeds their own weight. In a year, the entire upper layer of sand, several centimeters thick, passes through the intestines of the

Holothurioidea. An individual about 30 cm long passes 100-200 g of sand through its gut each day (Backus, 1973). In addition to the Holothurioidea and Gastropoda, the benthic sediment is also intensively consumed by many species of fish. Some 25 t of calcareous material passes through the intestines of fish feeding on the bottom sediments, periphyton, and corals on the reef off Panama each year for each ha, with a population density of these fish of 6 individuals for each 10 m^2 (Glynn, 1973).

The periphyton is the main food of most of the reef Gastropoda, as well as crabs, sea urchins and fish. The calcareous algae and corals are eaten by the parrot fish, which use their strong jaws to scrape the periphyton from the rocky base and dead corals (Randall, 1974).

The direct consumption of macrophytes by the reef fauna is relatively slight. The algae are partially utilized by certain gastropods, sea urchins, fish and Chelonia. Nevertheless, the macrophytes play an important trophic role in the reef community as a source of usable dissolved organic matter and detritus. The massive species of macrophytes (Thalassia, Sargassum, Syringodium, Chnoospora, Caulerp) cover significant areas. Photosynthesis in their stands on the reef may be as great as 10-20 g C/m^2 per day (Odum et al., 1959). The quantity of products of photosynthesis liberated by the macrophytes into the water amounts to 10-20% of the daily production (Khaylov, 1971). Consequently, the production of dissolved organic matter over the underwater meadows of macrophytes may be as great as 1-3 mg C/m^3 per day, which is sufficient for the feeding of many species of benthic and planktonic filter feeders, including corals. As a result of the death of the algoflora, a mass of detritus is formed (Goreau, Goreau, 1973); for example, on one island of the Great Barrier Reef, about 1 kg/m^2 per year. The main nutrient component of the detritus consists of the microflora and protozoa which inhabit it abundantly (Fenchel, 1970). The detritus serves as a source of nutrition for a rich detritophage fauna. Some of them collect the detritus from the bottom (gastropods, Holothurioidea, sea urchins, various Crustacea, Polychaeta, many fish) while others filter out the detritus stirred up by the surf from the water.

2.7 Conclusions

The materials analyzed above, concerning the structure of modern coral reefs, like the data from fossil reefs (Ladd, 1969; Copper,1974), show that the coral community forms a clear biogeocenosis, consisting of a system of specialized biotopes and their populations. This system is similar, even under greatly differing conditions, e.g., on barrier reefs, near large islands and continents, in highly productive waters with rich terrigenous runoff and in atolls in the oligotrophic waters of the trade currents. The reason for the similarity of the structure and level of productivity of the reefs in these various regions is that conditions in the coral communities, in contrast to communities of the pelagic zone, are controlled primarily not by external physiochemical, but rather by internal biological factors. The coral community constructs a specific limestone structure--the reef. It might be thought of as a kind of a cultivator, in which a definite spatial distribution of biocenoses is created, with a definite orientation regarding the flow of solar energy, protection from destruction by wave action, tectonic downwarping, etc. Given the relative constancy of the temperature in the tropics, the conditions of life in the reef community are regulated primarily by the influence of the intensive vital activity of its organisms. This is particularly true of the processes related to the cycle of nutrients, which are practically completely controlled in the reef by the community itself. The regulating influence of the community on environmental conditions makes them largely predictable, which, in turn, allows specialization of a significant portion of the flora and fauna (Grassle, 1973; Golikov et al., 1972).

These same properties of coral biogeocenoses apparently explain their unusually high productivity largely counteracting the limiting effect of the shortage of nutrients which limits the productivity of the aquatic ecosystems of the tropical zone. The primary portion of photosynthetic production of the reef is created under conditions of a semiclosed cycle of nutrients. These conditions exist in the host organisms of symbionts and in communities of periphyton organisms, where the producers and reducers are joined into a single structure. We must assume that this semiclosed cycle of biogens is characteristic to some extent for colonies of calcareous algae as well. These colonies have a porous surface, overgrown with microflora (DiSalvo, 1973), which can mineralize the organic phosphates liberated by the algae.

Another factor in the high productivity of the coral biogeocenosis is, apparently, the existence of extremely effective mechanisms for extraction and utilization of organic forms of nutrients from the ocean water passing over the reef. The mean content of organic forms of nutrients in the surface waters of the tropical zone of the ocean is 0.2-0.4 μg-atom/ℓ of phosphorus and about 1 μ-atom/ℓ of nitrogen, as great as the content in the water of the temperate zones (Sapozhnikov, 1971). Most of this matter is found in the composition of relatively stable dissolved organic matter which is utilized by the periphyton microflora of the reef in large quantities. Possibly, it is the presence of this external source of organic matter and nutrients which represents one of the main factors in the unusually rich development of periphyton on all solid surfaces and in the large-grained sediment of the reef.

The richness of the microflora of the bottom sediments depends directly on the degree of development of living corals in the biotope, whereas the development of the periphyton, microflora and algoflora do not depend on this factor (Sorokin, 1975b). The periphyton grows even in places where the corals have been completely smashed by a typhoon. The periphyton community of the reef, particularly in the frontal zone and on the surface of the reef flat, exists by utilization of nutrients and, to some extent, of the organic matter from the ocean waters passing over the reef.

Another portion of the organically bonded nutrients in the ocean water passing over the reef is present in the form of suspended organic matter, pseudoplankton, and plankton. The reef community actually is a powerful biological filter, capable of utilizing this source almost completely. The corals trap zooplankton and protozoa, the filter feeders and sediment feeders trap the phytoplankton and microflora. The high effectiveness of the reef as a biologic filter and the significant volume of neritic water which passes over the reef, with a high concentration of plankton, allow the coral community to receive such a great influx of organically bonded nutrients that it compensates for the unavoidable losses of nutrients liberated in the process of metabolism and carried away by the ocean water passing over the reef. The positive balance of nutrients in the processes of exchange between the reef and the water passing over it is apparently the key to the solution of one of the most baffling peculiarities of the reef metabolism: the clear accumulation of organic matter in the community, in spite of its visible and tremendous output into the waters of the ocean. It is clearly visible to the naked eye that the water approaching the reef is transparent, with little organic sediment, while the water flowing away from the reef is turbid, rich in suspended matter and organic aggregates (N. B. Marshall, 1968; Johannes, 1967). How is the essentially positive balance maintained, in terms of organic matter, with these losses and with the intensive destruction of organic matter within the community? Apparently, the reef community is so organized that, being under optimal conditions of illumination and temperature and having an unusually high content of chlorophyll per unit area, it creates a sufficient quantity of organic matter to compensate for losses due to erosion and destruction. We must consider that the organic matter which is lost and destroyed is poorer in nutrients than that consumed by the community from the water passing over the reef. Without this mechanism, providing a more positive balance of nutrients in exchange with the surrounding water, the formation of the coral biogeocenoses would hardly be possible.

It is characteristic of coral communities to have extensive porous surfaces, overgrown with an active and rich periphytonic microflora. Its functioning occurs under optimal conditions of temperature and oxygen supply. Under these conditions, similar to the conditions of the air tanks of purification structures, the processes of bacterial destruction are intensified, like chemical reactions on a surface of porous platinum. It can be assumed that the microbial population of the periphyton can assimilate those fractions of the organic matter which make up the predominant portion of the total dissolved organic matter of sea water, but are difficult for bacterioplankton to oxidize in the pelagic zone. Therefore, although the waters of the ocean passing over the reef show an increased content in labile organic matter (Sorokin, 1973b), it is probable that their content of a stable organic matter and particularly, the nutrients bonded with it, must decrease as the ocean water passes a reef.

This system of exchange of coral communities with the water passing over the reef requires further testing, but we can assume that, given the tremendous area of coral reefs, the intense destructive activity of the periphyton microflora is of global significance in processes of biogeochemical cycling of organic matter in the world ocean. The coral reef communities should be looked upon as the location of oxidation of a significant portion of the stable organic matter (water humus) in sea water. It should be expected that the constancy of concentration of organic matter in the waters of the ocean--about 2 mg C/ℓ--is controlled to some extent by the periodic passage of the entire volume of water in the world ocean over coral reefs as global circulation occurs. According to our calculations, the time required for this process is not so great in the geologic scale of time: about 40,000 years.

Investigators studying coral biogeocenoses report a high degree of maturity of the coral reef ecosystems (Grassle, 1973). The signs of maturity include the predominance of long-living forms with slow growth rates, as well as the high predictability of conditions of the growth medium and a high degree of specialization of many mass species which we mentioned earlier (Golikov et al., 1972). The maturity of the reef community is also revealed as we analyze the inherent complex interactions between organisms as, for example, the hierarchy of antagonistic interactions between corals (Lang, 1973), as well as the developed ecologic metabolism.

The maturity of the reef biogeocenosis is also manifested in the close energy interaction of the component communities. This interaction basically follows two paths. The first path is the transfer of dissolved organic matter liberated by autotrophs, detritus, periphyton and benthic bacteria and algae, washed by the surf from the epibiotic associations and bottom sediments. The tide currents over the reef are mostly of an advancing and retreating nature. As the tide rises, practically the same water which left the reef when the tide fell returns to it. At low tide, the water leaving the reef passes over its frontal slope, where an intensive multiplication of microplankton occurs, and is held there. Therefore, the corals and other benthic filter feeders and sediment feeders, living on the outer slope of the reef, can utilize the energy reserves of the organic suspended matter washed from the shallow zone of the reef. Another path in the trophic connection of the biotope of the outer slope with the shallow zone is the "runoff" of detritus, bottom sediments and clastic material in the direction of the fore-reef. At the same time, the corals and macroalgae growing abundantly on the outer slope enrich the water with dissolved organic matter, which is carried by the tidal flow into the shallow portion of the reef and there consumed by the periphyton microflora. We must, therefore, consider the point of view (Yonge, 1963; Ladd, 1969) that the biotopes of the outer slope of the reef are not connected in any way with the biotopes of the shallow portion of the reef (reef flat and lagoon) to be incorrect.

The complex and intensively functioning ecosystem of the coral reef is very sensitive to anthropogenic effects: pollution, eutrophication, overfishing. Pollution and eutophication result in a shift of the cycle of organic matter in the direction of predominance of destructive processes, decrease of the oxygen content, development of the process of reduction of sulfates to hydrogen sulfide, appearance of reducing sediment. All of this may cause massive death of corals and of the fauna which populate it, rapid development of macrophytes, *Zoantharia* and *Actinia*, which inhibit the growth of corals and replace them (DiSalvo, 1973; Banner, 1974; Sorokin, 1971b, Sorokin, 1973b). It is thought that the harvesting for their beautiful shells of large numbers of some gastropod mollusks such as *Hazonia tritonis*, which are the natural enemies of the sea star _Acanthaster planci_, has been one cause of the sudden increase in the number of these animals, which have consumed over hundreds of square kilometers of corals (Endean, 1973). Extensive harvesting of tridacna and trepangs reduces the biofiltration activity of the community and decreases the intensity of processing of bottom sediments. It is therefore necessary to turn the most serious attention to the protection of coral communities as one of the most important biologic systems of the ocean, and of the biosphere as a whole.

3. Fouling Communities.

(Ye. P. Turpaeva)

The term "fouling" is usually used to mean a complex of animals and plants, which settles onto artificial structures. The formation of fouling communities on structures submerged in the water depends on the capability of certain species of animals and plants to develop successfully in a situation created by man. The basic components of fouling communities include the attached forms: cirripedian crustaceans, bivalve mollusks, hydroids, Bryozoa, sedentary polychete worms, sponges, Tunicata, as well as certain algae. Furthermore, the overgrowth includes mobile animals: crabs, Nudibranchiata, errant Polychaeta, Nematoda, Harpaticoida, Pycnogonida. The total number of species of animals and plants recorded in the fouling communities reaches 2,000.

The qualitative composition of the fouling communities on all artificial substrates is determined by the composition of the flora and fauna of the surrounding regions, the number of species fouling being always less than the number of species inhabiting the region. The epibiotic fauna of the littoral regions usually number 50-100 species. The total number of species in macroscopic fouling communities in the open seas of the USSR is not over 25, in the southern seas--10. Fully formed fouling biocenoses in the southern seas of the USSR usually consist of 3-5 species (2-3 attached, 1-2 unattached), while the quantitative development of one of the attached species is usually significantly more than the development of the remaining forms. A similar peculiarity is characteristic of the oligomyctic benthic biocenoses. Epibiotic biocenoses represent an extreme case in this respect.

The species which settle in epibiotic associations usually reach significantly greater quantitative development than in natural biotopes; correspondingly, the total biomass of fouling biocenoses is usually great, frequently one or two orders of magnitude more than the biomass of natural communities. For example, the biomass of the fouling associations in the Sevastopol' Bay may reach 100 kg/m^2, the fouling associations of Balanus in Kerchenskiy Strait--40 kg/m^2, the fouling associations of hydroids in Taganrog Bay--15 kg/m^2 (Turpaeva, 1971).

The overwhelming majority of species of animals which compose these communities have a pelagic larval stage. The larvae of some mass species from these communities (numerous forms of bivalve mollusks, and cirripedian crustaceans, live in the plankton for rather long periods of time--up to several weeks). In temperate water, the breeding of fouling organisms stops in winter. They winter over in the mature stage, and begin to breed again in the spring, with the beginning of the development of phytoplankton. In accordance with this, the settlement of organisms and development of the epibiotic biocenoses are also seasonal processes. The larvae of the various species of animals settle at different temperatures, which defines the sequence of appearance of the various species in the composition of the fouling assemblages and determines the succession of these biocenoses (Zevina, 1972).

Thus, for the fouling communities, which develop in the internal seas and littoral oceanic regions, a small number of species (oligomyctic nature), a high biomass and the seasonal changes in the process of formation are peculiar.

Studies of fouling processes in the oceanic waters are only beginning. The formation of large masses of fouling in the open ocean is limited by the lack of a stable substrate. Although organisms which are not inhabitants of the littoral regions are always found on the hulls of ships which follow the transoceanic routes, the oceanic forms alone never develop on ship hulls. We can make judgments concerning the composition of fouling associations in various regions of the open ocean at the present time by studying driftwood. Materials collected from the northwest Pacific (Turpaeva et al., 1976) show that oceanic fouling communities are also characteristically oligomyctic, with a high biomass and seasonal alteration of composition, related not only to seasonal changes in the presence of pelagic larvae in the plankton, but also to changes in the overall flow of the currents.

In spite of the seasonal changes in the composition of fouling communities, their structure is always characterized by clear-cut domination by a small number of species. The species which are dominant in these communities are usually representatives of groups which are far removed from each other in the systematic and ecologic aspect (Turpaeva, 1967). In these communities, there is no competition among dominant species for food, and the negative effect which they have on each other is minimized.

An example of such a structure is the fouling community on the hydrotechnical installations of a metallurgical plant located at Zhdanov on the north coast of the Azov Sea. Six mass species have been found in this community: the hydroid Perigonimus megas, feeding primarily on the copepod Calanipeda aquaedulcis; the cirripedian Balanus improvisus, feeding on phytoplankton and small zooplankton; hydroid epibionts: the infusorian Zoothamnium sp. and the bryozoan Boverbankia imbricata, feeding, apparently, on microplankton and small detritus; the predatory nudibranchiate mollusk Tenellia adspersa and the euryphagous crab Rhitropanopeus harrisii.

Many years of study of the composition of this community and the ecologic-physiologic indices of its main species, both in nature and in the laboratory, have revealed various types of interactions among them.

A complete system of symphysiologic (B. N. Beklemishev, 1951) interconnections of this overgrowth community numbers some 40 direct and indirect topical and trophic links, most of which function during the spring and summer, when the larvae settle, the macroscopic epibiotic organisms grow, and the community as a whole is formed. The various connections of this system are not equal in terms of their time of action, nature of effect on the population of dependent species or intensity. The diagram (Fig. 6) shows the 16 most important connections within this system.

The dominant species of the biocenosis is the hydroid. The second species, in terms of abundance, is the *Balanus*. They usually settle in May and develop simultaneously. Under favorable conditions, with a favorable quantity of plankton food, the hydroid forms a thick cover on the substrate within a month. Its branching stolons cover the *Balanus* and hinder their access to the water and food--paired, indirect, topical and tophic connection 1 develops, reducing the growth rate and, later, the population of *Balanus*. Soon, *Vorticella* develop on the stolons of the hydroid (direct topical connection 2) and the suppression of the *Balanus* is increased (connection 3). The population of the *Vorticella* on the stolons of the hydroids is regulated during this period by its intraspecific indirect topical connection (4). In June, the *Tenellia* appear in the community. They live on the stolons of the hydroids and feed on the hydroids and *Vorticella* (direct topical and trophic connection 5 and direct trophic connection 6). With a low population of *Tenellia*, its food demands are met almost entirely by eating the *Vorticella*, thus protecting the hydroids from being eaten by the *Tenellia* (indirect trophic connection 8). If the population of *Tenellia* is high, it not only eats out the *Vorticella*, but also suppresses the development of hydrants to the extent that some portions of the colony having none of them die and separate from the substrate. This improves the conditions of nutrition of the *Balanus*, creating an indirect trophic connection between the *Tenellia* and *Balanus* (7). The suppression of the hydroids decreases the area of the substrate and the quantity of food for new generations of *Tenellia*. The *Tenellia* population is regulated by paired indirect connection 9, as a result of which, some of its individuals are expelled from the hydroid colony and carried away from the community by the flow of the water. In late June, the bryozoan *Boverbankia* appears in the community, overgrowing the stolons of the hydroids (direct topical connection 10), partially expelling the *Vorticella* (indirect topical connection 11). In July, crab larvae begin to settle. The young crabs grow rapidly, and are quite voracious. They eat the *Vorticella* and Bryozoa (connections 13 and 14), and the Calanipeda which they find among the hydroids, mysids hiding among the stolons of the hydroids, their own juveniles (connection 16) and quite eagerly eat the *Tenellia* and its clutches of eggs (connection 15). After the crab appears, the population of *Tenellia* decreases rapidly, and, therefore, the damage done by the *Tenellia* to the hydroids also decreases. Since the predator has disappeared, the hydroid once again begins to grow and, during the autumn development of zooplankton, the colonies grow and multiply.

In order to even approach a quantitative evaluation of some of the connections in this system, we utilized the method of mathematical planning of experiments, which allowed us to vary the number of species of animals interacting in the experiment. The experiment was undertaken with four species--the hydroid, *Balanus*, *Vorticella* and *Tenellia*. We studied the strength of the connections relating to two complexes: suppression of the *Balanus* by hydroids (complex I) and the interaction of the hydroid with the *Tenellia* (complex II). The experiments were

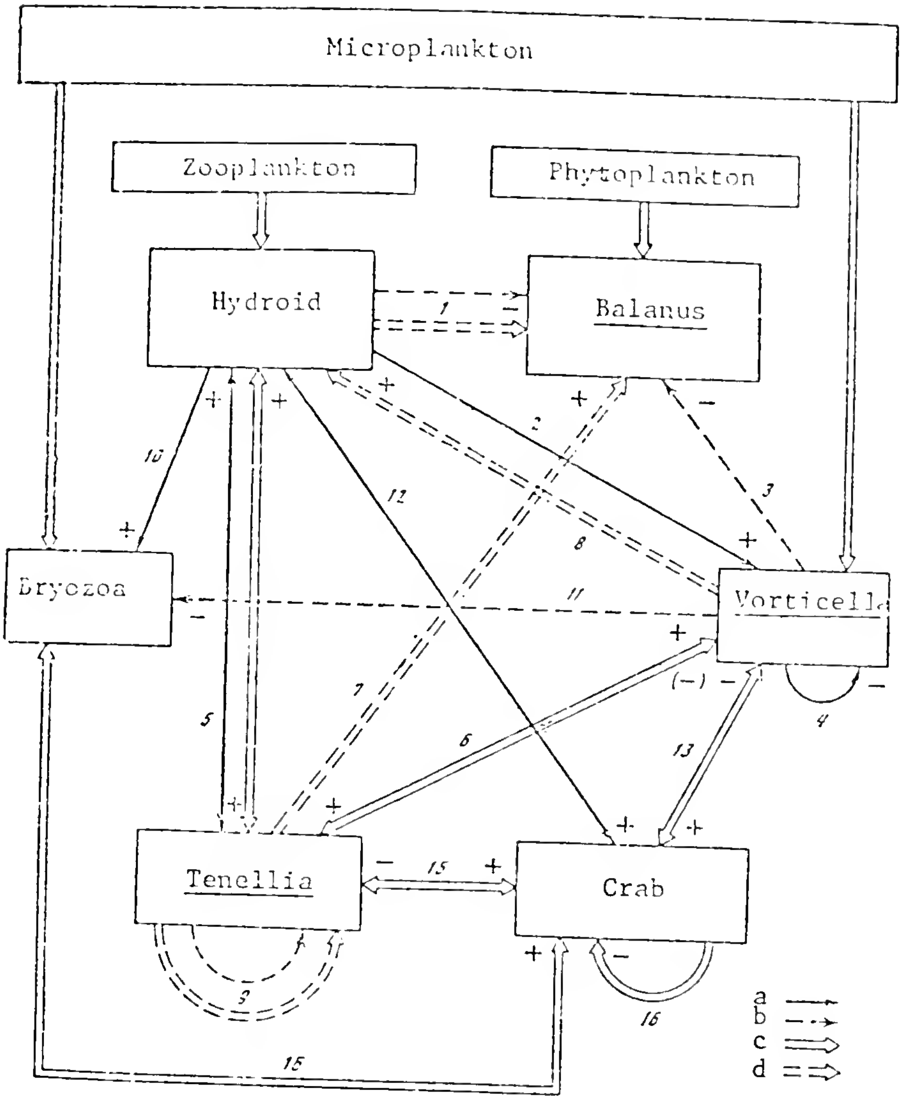


Fig. 6. Diagram of symphysiologic connections of an overgrowth community in the Azov Sea. Connections: a, Direct topical; b, Indirect topical; c, Direct trophic; d, Indirect trophic. Arrows point to species, the abundance of which is changed under the influence of the given connection. A double-ended arrow indicates that the abundance of populations of both species changes. The signs by the arrows indicate the nature of the influence of the connection on the population of the species: + indicates an increase, - indicates that the abundance of populations of both species changes. The signs by the arrows indicate the nature of the influence of the connection on the population of the species: + indicates an increase, - indicates a decrease. The numerals show the connection numbers.

organized according to the plan of a full factor experiment (FFE-2^3), the experimental object was the *Balanus*, the factors were the *Vorticella*, tenellia and hydroid. In accordance with the planning matrix, each factor was represented at two levels: the upper (+) and lower (-) levels. For the *Tenellia* and hydroid, the lower level represents absence of the species in the corresponding versions of the FFE, while the upper level represents its presence. The *Vorticella*, in versions with a lower level, was periodically eliminated. The plan and results of the experiment are presented in Fig. 7. As we can see from the graph, significant suppression of the *Balanus* is observed only in those versions in which the hydroid developed; the hydroid and *Vorticella* developed well only when the *Tenellia* were absent, while a high population of *Tenellia* was formed where the hydroid was present and the *Vorticella* was periodically eliminated.

The results of the experiment allowed us to calculate the relative intensity (ratio of value of partial effects to results of experiment in those versions in which effect of given connections has been revealed) of the connections which we modeled (Table 9). It was found that the coefficients of relative effectiveness ξ for the various connections are not the same, and change from comparatively small positive to high negative values. For bilateral connections, the two coefficients of relative intensity differed not only in magnitude, but also (in two cases) in sign. The higher the value of negative coefficient ξ, the greater the suppression of the dependent species; the higher the value of the positive coefficient, the more favorable the conditions for development of the dependent species; the lower the modulus of coefficient ξ, the weaker the effect of the connection.

The values of coefficients of relative intensity produced for the connections modeled were compared with the characteristics of development of the animals or the status of the populations. To do this, using the results of the FFE, we calculated the specific rate of weight increase (C_w) of the *Balanus* and hydroids. We found that the specific rate of growth of the *Balanus* changed as a function of the specific growth rate of the hydroid (Fig. 8). The suppression of the *Balanus* was weakest when the three-member connection 7a was functioning (Fig. 7, version 8) with C_w of the hydroid less than 0.3. An increase in the specific growth rate of the hydroid to about 0.4 was accompanied by a severe inhibition of the growth of the *Balanus*. Comparison of the coefficients ξ of the connections of complex I with the values of C_w for the hydroid showed that the growth rate of the *Balanus*, with low growth rate of the hydroid (less than 0.3), was determined by the conditions under which the animals were maintained. With a further increase in C_w of the hydroid, the effect of symphysiologic connections appeared, the intensity of which increased with an increase in the growth rate of the hydroid. In turn, the specific growth rate of the hydroid changed as a function of the *Tenellia* population (connection of complex II). Eating the hydroid, the *Tenellia* constantly damages the hydranths, penetrating their cover and sucking out the plasma. The damaged hydranths regenerate after 3 or 4 days, but until this happens, the total food intake of the hydroid colony decreases, and its growth is slowed. The frequency of damage, obviously, is related to the population density of the *Tenellia*, which can be estimated by the weight of the hydroid colony

Table 9. Characteristics and relative intensity of symphysiologic connections in an overgrowth community as modeled in a full factor experiment.

Complex	No.	Characteristics of connections	Interacting species			Coefficient of Relative effectiveness ξ
			Conditioning	Dependent	Modifiers	
I	1	Indirect topical-trophic	Hydroid	Balanus	-	-0.58
	3	"	"	"	Vorticella	-1.35
	7	"	"	"	Vorticella, Tenellia	-0.39
	7a	"	"	"	Tenellia	-0.07
II	5	Direct topical-trophic	Tenellia Hydroid	Hydroid Tenellia	- -	-10.02 0.43
	6	"	Tenellia Vorticella	Vorticella Tenellia	- -	0.12 0.50
	8	Indirect trophic	Tenellia Hydroid	Hydroid Tenellia	Vorticella "	-0.61 0.98
Intra-specific connec-tions	4	Indirect	Vorticella	Vorticella	-	-9.00
	9	Indirect topical-trophic	Tenellia	Tenellia	-	-27.62

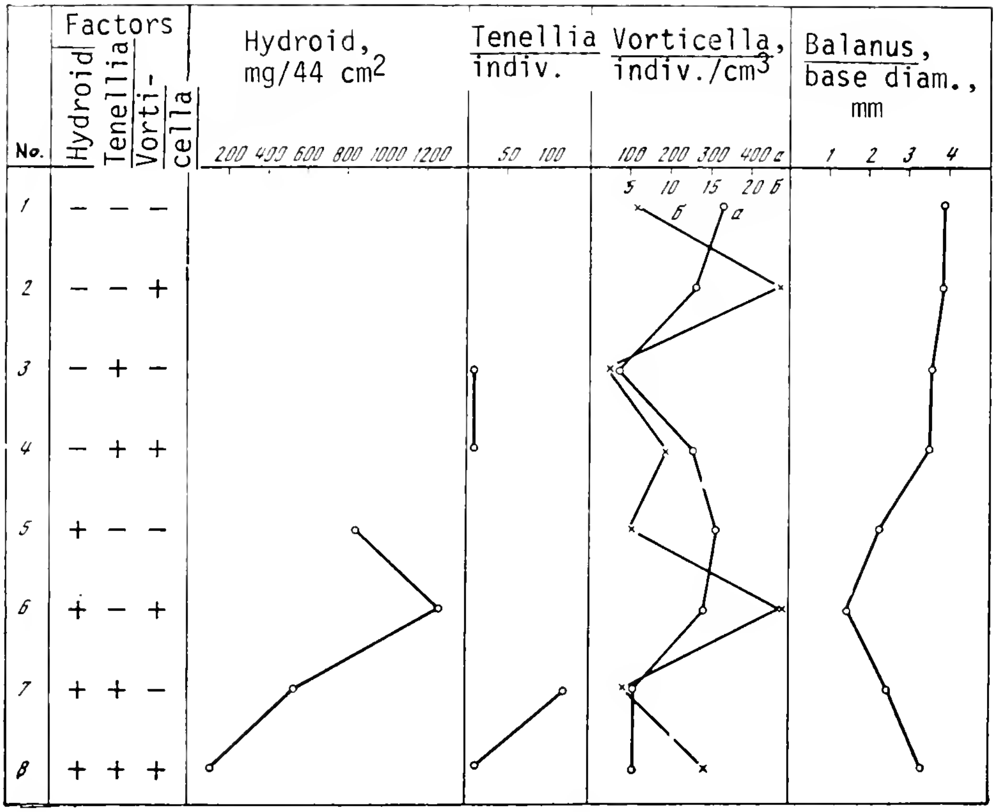


Fig. 7. Change in abundance of hydroid, Tenellia, Vorticella and Balanus in various versions of a full factor experiment FFE-2³. Number of individual infusoria (a) and colonies (b) counted for Vorticella.

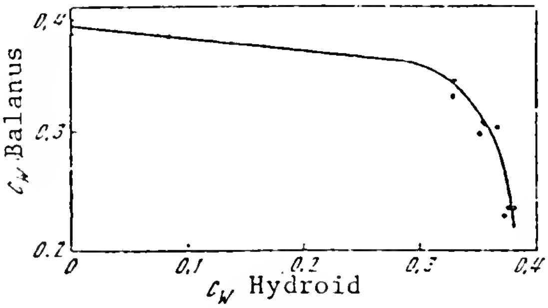


Fig. 8. Relation of specific growth rate of Balanus to specific growth rate of hydroid.

per individual mollusk. The variations of this quantity were found to be slight: In version 7, each mollusk corresponded to about 6.5 mg of hydroid, in version 8--about 3 mg. However, the specific growth rate of the hydroid in version 7 was only 15% less than the control, while in version 8 it was almost 70% slower, and the relative intensity of connections 8 and 5 differed by a factor of 16 (-0.61 and -10.02).

The influence of symphysiologic connections of both of the complexes studied was thus manifested in a very narrow range of change of the effective factor--the specific hydroid growth rate (complex I) and the relative *Tenellia* population density (complex II)--within limits confined to the "effective range" of the complex of connections. Outside the limits of this range, with a lower intensity of the effective factor the influence of the connections is not felt, and the development of the dependent species is determined by its ecologic peculiarities under the specific conditions at hand; with higher intensity of the effective factor, the dependent species is destroyed. In turn, changes in the intensity of the effective factors are determined by the presence of modifier species: the *Vorticella* and *Tenellia*. The intraspecific connection coefficients of both these species were found to be much higher than the interspecific connection coefficients. This agrees with the ecologic theory, according to which intraspecific competition, with high populations, is more acute than interspecific competition (Shorygin, 1939, 1946).

Long-term changes in the intensity of connections can be presumed in those cases when a slow increase in biomass or abundance of the conditioning species occurs. However, a high abundance or biomass of a conditioning species cannot be used as an indication of great intensity of a connection. According to the materials of the FFE, the greatest value of relative intensity was that of connection 5 (version 8), where the population of the conditioning species (*Tenellia*) was quite low throughout the entire experiment, while the development of the dependent species (hydroid) was suppressed at the very beginning. The symphysiologic connections with high intensity of action modeled in the FFE rapidly stopped the growth of the population of the dependent species by its elimination; connections with low intensity acted slowly, and the dependent species continued to develop.

In the natural overgrowth community, the symphysiologic connections modeled in the FFE function at different times. The time divergence of the action of the various connections is caused, on the one hand, by the seasonal differences in the time of settling of larvae, determining the seasonal succession of complexes of the connection, and, on the other hand, by time differences in occurrence of the maximal abundance of the various species of animals, defining the sequence of functioning of the connections of each complex. For example, in spring, after settling of the hydroid and *Balanus* larvae, when the young stolons of the hydroid are free of epibionts, the action of connection 1 is evident. After some time has passed, the *Vorticella* develops on the 4 to 6-day old stolons of the hydroid, and connection 3 begins to function, which, with intensive development of the hydroid, usually causes mass mortality of the young *Balanus*. In mid-summer, with mass development of the *Tenellia*, connections begin to function which suppress the hydroid; at first connection 8, decreasing the growth rate of the colonies, then connection 5, suppressing its vital activity. As the *Tenellia* population increases, intraspecific connection 9 begins to function, the intensity of which apparently gradually increases. After the vital activity of the hydroid is suppressed, the intensity of connection 9 reaches its maximum, most of the individual *Tenellia* are expelled from the community, and the remaining small portion, temporarily go over entirely to feeding on Vorticella, until the hydranths regenerate (connection 6). Thus, in the overgrowth community investigated, a sequential change is observed in the effect of weak and strong symphysiologic connections. During functioning of the weak connections, the abundance and biomass of the dependent species increase. During functioning of weak positive connections, the increase of abundance and biomass is determined by the ecologic peculiarities of the species (fertility, growth rate, rate of settlement of larvae). The effect of weak negative connections is superimposed on the effects of these peculiarities, and the development of the abundance and biomass of the dependent species is retarded. Strong negative connections cause a sharp decrease in the abundance of the dependent species.

It can be assumed that the sequence of functioning of connections and alternation of weak connections, acting slowly, and strong connections of brief duration, combine to determine the oligomyctic nature of the overgrowth community and sharp changes of their dominant species with time.

4. Benthic Shelf Communities (A. A. Neyman)

In this section, we shall discuss benthic shelf biocenoses beyond the limits of the plant zone, i.e., at depths of over 10 m.

The food resources of the inhabitants of this zone consist of the detritus which reaches the bottom layers of water and the floor from the photic layer. This greatly simplifies the composition of the benthic shelf biocenoses, since producers and phytophages are absent, while the detritus consumers remain (see III.5), along with the low-mobility predaceous forms.

Quantitative investigations of the benthos in large water areas are performed using bottom samplers, which trap only the non-moving and slowly moving animals. Therefore, bottom-sampler collections can be used only to study the competitive relationships between animals of a single trophic level. Predator-prey relationships are played out between representatives of the low-mobility benthos and necton (benthophagous fishes) and migrating benthos (e.g., crabs), i.e., they go beyond the framework of the biocenoses which can be studied by means of bottom samplers (L. G. Vinogradov, 1963; Vinogradov, Neyman, 1965).

V. P. Vorob'yev (1949) suggested a method of differentiating biocenoses according to species dominant in terms of biomass. This method has been widely used in Soviet marine research. The method of V. P. Vorob'yev is quite simple and, at first glance, quite formal: in a bottom-sampler sample, the species which dominates in terms of biomass is determined; stations at which the same dominant species is found are combined into a biocenosis. If these stations are placed on a map, as a rule, we find that stations relating to a single biocenosis are quite regularly placed (A. P. Kuznetsov, 1963, 1970; Neyman, 1963a, 1971). Station-by-station comparison of the benthos with data on the particle-size distribution of the bottom deposits reveals (Neyman, 1963b) that each biocenosis is characterized by its own type of particle-size distribution, and the particle-size distribution differences of similar biocenoses (within a single trophic zone) are quite clear, though not great: The same size fraction of bottom soil predominates, but the degree of dominance and fraction of the corresponding particles differ (Fig. 9). Thus, a biocenosis distinguished by the method of V. P. Vorob'yev is a natural formation, owing its development to fine differences in the process of sedimentation within the limits of a single trophic zone.

N. P. Bubnova (1971, 1972) studied the process of nutrition of two detritophagous bivalve mollusks in the White Sea--*Macoma baltica* and *Portlandia arctica*--inhabiting soils with different contents of clay particles. She demonstrated that the association with different soil types of these mollusks was directly related to differences in their capability to sort the bottom deposits: *Portlandia* cannot live on

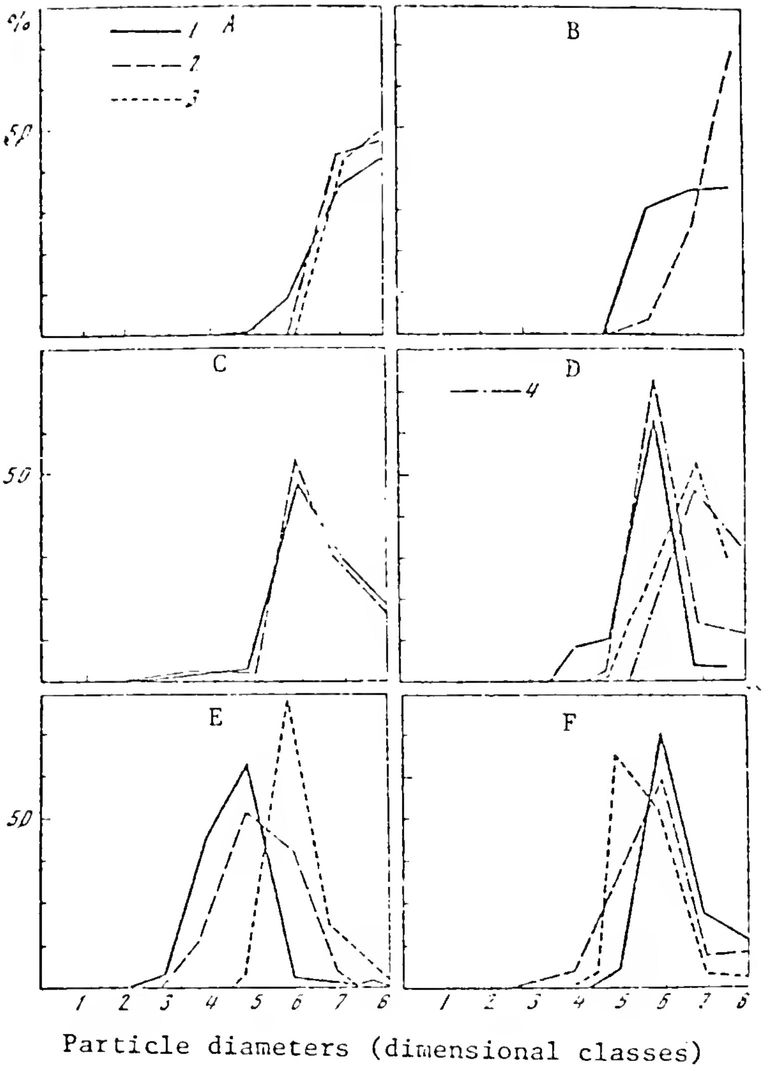


Fig. 9. Relationship of particles of various diameters in soils in bottom sections occupied by different biocenoses. Particle diameter, mm: 1, >2; 2, 2-1; 3, 1-0.5; 4, 0.5-0.25; 5, 0.25-0.1; 6, 0.1-0.05; 7, 0.05-0.01; 8, <0.01. Biocenosis A: 1, *Macoma calcarea*; 2, *Yoldia hyperborea*; 3, *Megayoldia thraciaeformis*. B, *Nuculana pernula*: 1, in Bering Sea; 2, in Gizhiginskiy Bay of the Sea of Ohotsk; C: 1, *Ophiura sarsi*; 2, *O. leptoctenia*. D: 1, *Brisaster latifrons*; 2, *Chiridota ochotensis*; 3, *Sternaspis scutata*; 4, *Axiothella catenata*. E: 1, *Venericardia crebricostata*; 2, *Serripes groenlandicus*; 3, *Clinocardium ciliatum*.

coarse-grained soil, due to its weakly developed apparatus for soil sorting, meaning that it cannot receive a sufficient quantity of food there. L. V. Sanina (1975), using the example of sestonophagous mollusks of the northern Caspian, showed that their distribution also depends on the ability to sort organic particles from a suspension with varying contents of mineral particles.

The use of the method of V. P. Vorob'yev, in combination with the study of the ecologic habit and methods of feeding of the main species making up biocenoses, has led to the conclusion that the core of a biocenosis consists of minimally competitive species, (Birshteyn, 1947; Vorob'yev, 1949; Ivlev, 1955; A. P. Kuznetsov, 1960; Sokolova, 1960; Turpayeva, 1948, 1949; Shorygin, 1955), because of the membership of the primary species of the biocenosis in different trophic groupings. The simultaneous existence of representatives of various trophic groupings is possible because they feed from different zones (levels) of the bottom sediments. Depending on which of the feeding zones contains the greatest quantity of nutrient substances in a given biotope, one or the other trophic grouping will be dominant in the biocenosis. The greatest competition occurs between representatives of the same trophic grouping.

However, there are biocenoses, the core of which consists of species of a single trophic grouping. Ye. P. Turpayeva (1948, 1949) has suggested that there may be fine differences in the nature of feeding of species of a single trophic grouping, although she had comparatively little data to work with. A. P. Kuznetsov (1960, 1963) is of the same opinion. At the present time, a great deal of material has been accumulated concerning the composition of shelf biocenoses of the seas of the USSR and other regions of the world ocean, and these statements can be made specific. For example, on the shelf of the eastern portion of the Bering Sea, there is an extensive zone of sedimentation at a depth of 50-150 m. The conditions are right there for rapid development of detritophages, particularly gatherers. Extensive areas of the bottom are occupied by biocenoses of *Macoma calcarea*, *Yoldia hyperborea*, *Nuculana pernula* and *Nucula tenius*, and in each of the biocenoses, all of these four species are included in the core of the biocenosis. They are all gathering detritophages. This composition of detritophage biocenosis is, obviously, a result of the abundance of food at their feeding level--detritus on the surface of the bottom deposits. K. N. Nesis (1965) believes that an abundance of food at a given feeding level leads to the appearance of biocenoses with a trophically homogeneous core. This is proved, perhaps, by the fact that these same biocenoses on a narrow shelf with relatively little sedimentation, have a different core composition, containing sestonophages and nonselective detritophages, as can be seen in the example of the biocenosis of *Macoma calcarea* in the eastern Bering Sea and eastern Kamchatka.

Eastern Part of Bering Sea

Position as to Biomass	Type of Feeding
1. *Macoma calcarea*	Gathering
2. *Yoldia hyperborea*	"
3. *Nuculana pernula*	"
4. *Nucula tenius*	"

Eastern Coast of Kamchatka

Position as to Biomass	Type of Feeding
1. *Macoma calcarea*	Gathering
2. *Clinocardium ciliatum*	Sestonophage
3. *Nicomache limbricalis*	Swallowing
4. *Ampelisca macrocephala*	Sestonophage

Analysis of the composition of biologically homogeneous biocenosis cores shows that their composition practically never includes more than one species of the same genus--a rule noted by Elton (1946). Similar species apparently have similar types of feeding, this similarity being expressed not only in that they feed from a single source of food, but also in that their method of capture of food and other peculiarities are similar. In other words, similar species belong to a single life form and occupy a single ecologic niche. Similarity of the nature of feeding of closely related species is confirmed by the analysis of association of two pairs of similar species (*Yoldia hyperborea* and *Megayoldia thraciaeformis*; *Ophiura leptoctenia* and *O. sarsi*) in the eastern Bering Sea with types of bottom: The biocenoses of species of each pair are found in this area on practically identical bottoms (Fig. 9). Competition in this case is avoided due to the spatial separation of closely related species, which have different zoogeographic association and inhabit zones where different water masses are in contact with the bottom (Neyman, 1963a). The theory of parallel communities is based on the spatial divergence of similar species (Thorson, 1957) in which representatives of one life form, but with different requirements for temperature or salinity, dominate.

Thus, even an abundance of food, leading to the development of a core of a biocenosis of species of the same trophic grouping does not eliminate the need for the species to differ as to type of feeding. For sestonophages, the possibilities for food differentiation are great, if only because they can be rather finely divided as to levels. The swallowing detritophages can also be divided in the same way--they can feed from the bottom, burrowing into it to various depths. Gathering detritophages do not have this capability--they can feed only from the surfaces of the bottom. Therefore, difference in the nature of feeding of gathering detritophages included in the core of a biocenosis must be quite precise. This leads to yet another rule: The core of biocenoses consisting only of gathering detritophages includes representatives of only one zoogeographic or, in the language of G. V. Nikol'skiy (1947), faunistic complex, probably because in order to achieve the precise differentiations in feeding, long-term joint existence in the zone of contact with the bottom of a single water mass is required.

The regularities outlined above concerning the composition and distribution of benthic biocenoses were obtained upon detailed study of benthic biocenoses on the shelves of arctic and boreal waters. Analogous data concerning the shelves of Antarctic waters are sparse. However, on the shelf and in the fjords of the south Orkney Islands, basically the same composition of biocenoses and the same variation of their distribution with the nature of the benthos of the tropical shelves differs from that of the subpolar shelves in that there are significant sections where the trophic zonality is disrupted or where the detritophages, particularly swallowing detritophages, disappear from the composition of the benthos. The same differences have also been noted in the composition of biocenoses. Whereas in the shelf biocenoses of the subpolar waters, all trophic grouping of nonpredaceous benthic invertebrates are practically always represented, in the shelf biocenoses of the subtropical and tropical waters, usually only one or two trophic groupings are present.

5. The Trophic Structure of the Benthic Population of the Shelves. (A. P. Kuznetsov, A. A. Neyman)

In recent decades in Soviet oceanography, studies of the trophic characteristics of the benthic population have been greatly developed. Domestic expeditions have accumulated significant materials (over 3000 samples) of the bottom population of the shelves of the world ocean, collected by a single methodology--by means of the "Okean" bottom digger. This allows us to make a judgment concerning the peculiarities of the composition and distribution of the benthos at depths from 10-20 m down to the upper levels of the slope (300-500 m) (Neyman, 1971). The studies have encompassed all geomorphologic types of shelves in various geographic zones.

The detailed studies of Ye. P. Turpayeva (1953, 1954) allowed her to work out a classification of marine benthic invertebrates on the basis of the source and method of capture of food. Studying the bottom population of the Barents Sea, Ye. P. Turpayeva distinguished the following trophic groupings: "swallowing"--inhabiting the surface layers of bottom deposits and swallowing the bottom whole; "gathering"--gathering detritus from the surface of the bottom; "A filterers"--feeding on matter suspended in the thin layer of water along the bottom; "B filterers" (active filter feeders)--feeding on layers of water located higher above the floor; "waiters"--receiving their food from the same layer as B filterers, but passively.

The nonpredaceous benthic invertebrates feed on the organic matter suspended in the water or in bottom deposits; therefore, the quantity of food available to them in any given section of the bottom is directly dependent on the productivity of the overlying photic layer. The abundance of food for predaceous animals (benthophagous fish, large crustaceans, etc.) depends on the distribution of nonpredatory invertebrates. Therefore, in studying the connection of the distribution of benthos with oceanographic characteristics (biotic and abiotic), we must first turn our attention to the peculiarities of the distribution of nonpredaceous benthic invertebrates, the first consumer link in the detrital food chain.

Ye. P. Turpayeva has shown that the distribution of biocenoses with predominance of swallowing and gathering animals, in terms of weight, is positively correlated with the content of fine fractions of bottom sediments, biocenoses with predominance of "A filterers" are correlated with the content of middle-sized fractions, biocenoses with predominance of "B filterers" and "waiters" are correlated with the larger fractions. Further study of the groupings has involved their spatial distribution. A. I. Savilov (1961) traced the regularities of their placement in the Sea of Okhotsk. In separating ecologic groupings, he utilized information on the sources of food, methods of its capture, degree of mobility of animals and methods of their attachment to the bottom. The study of the spatial distribution of trophic groupings required simplification of the classification. M. N. Sokolova (1956, 1960) used only the source of food as a criterion for differentiation of trophic groupings, and distinguished three groupings: detritophages, unselectively swallowing the bottom and feeding on buried detritus from the uppermost layers of the bottom; detritophages which collect detritus from the surface of the bottom; and sestonophages, which consume suspended detritus.

The distribution of trophic groupings was found to be directly related to the mode of sediment accumulation which determines whether the main portion of the detritus will be suspended in the lowest layers of water, or precipitated onto the surface of the bottom, or buried in the bottom. This allowed M. N. Sokolova (1964, 1966) to formulate the concept of the trophic zone. The trophic zone refers to a section of the bottom occupied by biocenoses of a single trophic type, i.e., with predominance (by weight) of a single trophic grouping. The trophic zone in all its parts is charcterized by similar conditions of feeding for benthic invertebrates, i.e., by a similar type of distribution of detritus.

The conditions for predominance of sestonophages arise when the erosion or transfer of sediment predominates over its precipitation. Conditions for predominance of detritophages of both groups arise when the process of precipitation of particles predominates over a given section of the bottom (Turpayeva, 1954; Sokolova, 1956, 1960).

Analysis of the data on the development of trophic zones on the shelves of the seas of the USSR, the particle-size composition of bottom deposits and the content of organic matter in them has allowed us to reveal the interrelationship between these characteristics. Based on them, a hydrodynamic regionalization of the Barents, Karsk and Okhotsk Seas was performed, based on the relationship of areas of the bottom occupied by various trophic zones (A. P. Kuznetsov, 1970, 1974). It was found possible to distinguish the types of shelves according to the predominant type of dynamics of the water, i.e., the fraction of the bottom area occupied by a given trophic zone (A. P. Kuznetsov, 1974; Kuznetsov, Neyman, 1975). The following types of shelves were distinguished: 1) shelves with active dynamics of the waters near the bottom; 2) shelves with weakened dynamics of the waters near the bottom; for both types, we can assume that the dynamics of the waters near the bottom are identical throughout their entire area; 3) shelves where there is spatial heterogeneity in the distribution of the dynamics of the waters near the bottom. Shelves of type 1 are narrow and steep, entirely occupied by zones in which sestonophages predominate. They include the shelves of the island arcs with clear predominance of attached sestonophages. In these areas, in places where silty sediment accumulates, we also find detritophages. Shelves of type 2 are ideally occupied by a single zone of predominance of detritophages. This type includes the shelf of Hudson Bay, with its long ice-covered season, reducing wave mixing, its characteristic bottom configuration and relatively mild tidal fluctuations of the level. It can be expected that the reduced dynamics of the waters near the bottom are characteristic for other seas in the Arctic as well. The Baltic Sea, in which detritophages sharply predominate, is of this same type (A. P. Kuznetsov, 1963, 1964, 1970, 1974). Shelves of type 3 are shelves on which, depending on their width and steepness, the direction of prevailing currents and the distribution of benthic deposits, we find the corresponding development of zones of predominance of all three trophic groupings.

Trophic zones which depend on the sedimentation mode are distributed just a regularly as zones of erosion and accumulation of sediments. M. N. Sokolova (1960) showed, using the example of the northwest Pacific, that they most frequently alternate vertically, following the bottom relief. On convexities of the bathymetric curve, zones of predominance of sestonophages usually develop; in concavities--zones of predominance of gatherers, and deeper--swallowing detritophages. On the next, deeper, convexity, a zone of predominance of sestonophages appears once more, etc. Thus, a set of three trophic zones is placed vertically one above the other.

Shelves differ as to width and steepness (Fig. 10). On all shelves, the shallows are occupied by sandy or rocky soils, allowing the development of zones of sestonophages (mobile or attached) in these areas. Deeper, depending on the width and steepness of the shelf, a zone of sedimentation is developed to some extent (Gershanovich et al., 1974) with predominance of gathering or swallowing detritophages. It may occupy various areas of the bottom, the predominance of detritophages may be expressed to varying degrees--from slight domination (40-50% of the total biomass) to complete domination (over 95%). One regularity is found which has not at present been fully explained. On broad shelves with a well-developed zone of sedimentation, the finest clayey silts are dominated by collecting detritophages, while swallowing detritophages predominate on somewhat coarser silts. On narrower shelves, where the zone of sedimentation is not so broad, the very finest silts are dominated, not by collecting, but rather by swallowing, detritophages (A. P. Kuznetsov, 1963; Neyman, 1963a).

As a rule, the vertical trophic zonality is expressed rather fully on shelves, which is facilitated by the currents directed along the edges of the shelf. Sometimes, the influence of the relief on the distribution of trohic zones may be buried by that of other factors. For example, if the currents are directed across the shelf, the vertical trophic zonality may be distorted, to the point of appearance of spottiness in the distribution of trophic zones (A. P. Kuznetsov, 1970). However, the relationship of distribution of trophic zones with the mode of sediment accumulation is fully preserved--in these cases, the zones of erosion and sedimentation are also distributed in spots (Sokolova, Neyman, 1966).

All of these conclusions were reached in a study of the benthos of shelves located under subarctic waters. Upon transition to a study of subtropical and tropical shelves, cases were noted which did not fall within the system described above. Here, the concept of eutrophic and oligotrophic types of trophic structures suggested by M. N. Sokolova

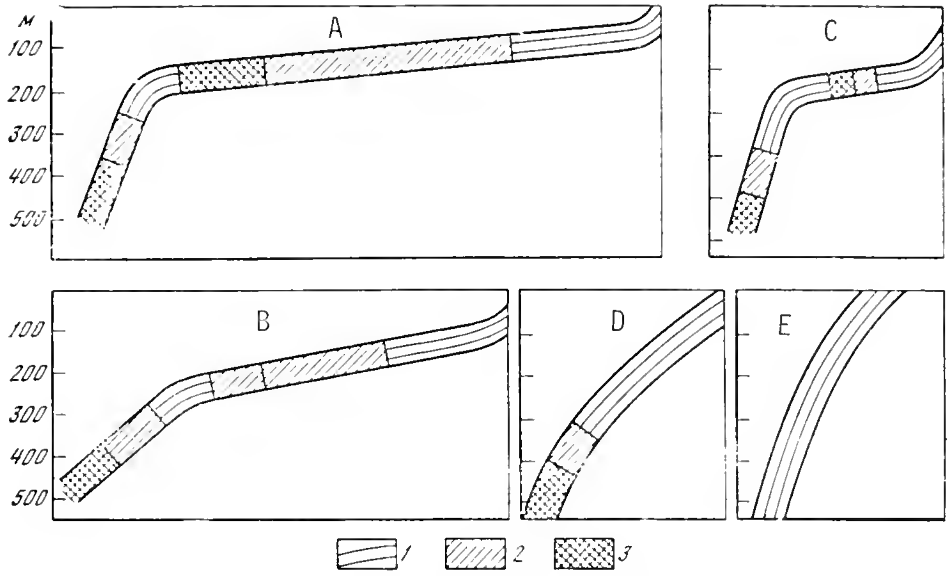


Fig. 10. System of distribution of trophic zones on shelves of varying widths and steepnesses. Shelf width not drawn to scale. 1, Sestonophages; 2, Gatherers; 3, Swallowing detritophages.

(1966, 1969, 1972) for the deep water benthos were found to be useful. A eutrophic structure is formed where the pelagic community is rather productive and the rate of sediment accumulation is high. These factors determine the abundant supply of the surface layer of sediment with organic matter and its rapid burial in a condition suitable for consumption by detritophages. An oligotrophic benthos structure is formed where the surface waters are more or less fully stratified, the pelagic community is low in productivity, the rate of sediment accumulation is very low. These factors cause the bottom sediment to be supplied with little organic matter, which is buried in a condition unsuitable or poorly suitable for utilization by detritophages.

A eutrophic structure results in practically 100% occurrence of representatives of the three trophic groupings and the appearance of a zone of dominance of each one under the corresponding conditions of dynamics of the bottom waters. With a eutrophic structure, the correlation in distribution of the trophic zones with bottom relief and the nature of the bottom deposits is quite clearly seen (Fig. 11a). An oligotrophic structure results in low occurrence of gathering detritophages, with still lower occurrence of swallowing detritophages; absence of a trophic zone of swallowing detritophages and weak development of a zone of gathering detritophages; universal development of a zone of dominance of sestonophages, depending little on bottom relief (Fig. 11b).

In the first approximation, it can be considered that the factor of rate of sediment accumulation acts identically throughout the shelf; therefore, in large-scale regionalization of shelves, we can abstract ourselves from circumcontinental zonality in the mode of sediment accumulation. On the shelf, only one set of three trophic zones is usually found (Neyman, 1963b, 1967), so that in large-scale

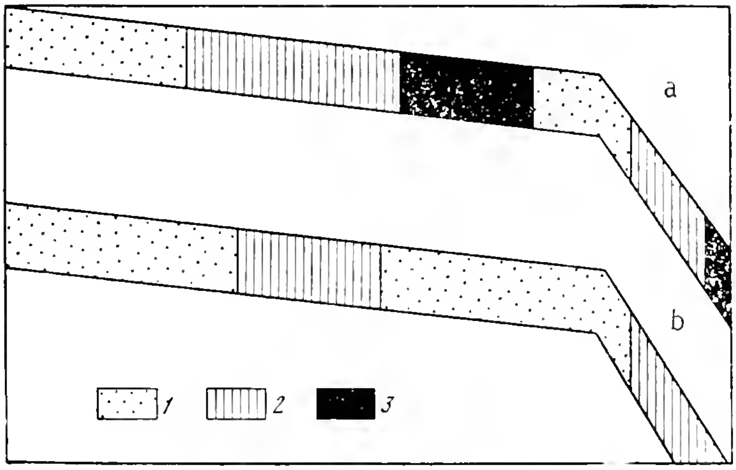
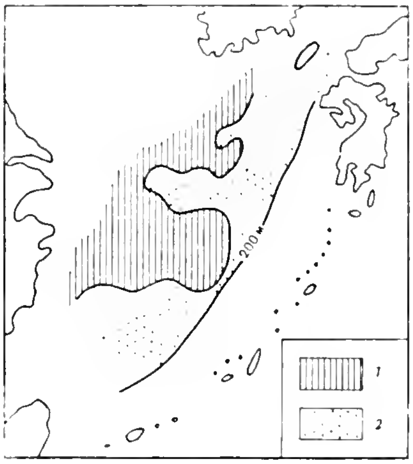


Fig. 11. Diagram of trophic zonality over a broad, flat shelf under eutrophic (a) and oligotrophic (b) conditions. Zone of dominance of 1, Sestonophages; 2, Gatherers; 3, Swallowing detritophages. Not drawn to scale.

regionalization of the shelves, we can also abstract ourselves from vertical zonality. The influence of the productive properties of the shelf waters on the characteristics of the bottom population remains to be studied.

The first attempt to analyze the trophic structure of the benthos on the example of the shelves of the eastern portion of the Bering Sea and the East China Sea (Neyman, 1969b) led to the conclusion of the decisive influence of the productivity of the waters on the trophic structure of the benthos. Both of these shelves are broad, flat shelves, with a well-developed zone of sedimentation in their central portion. The benthos of the East Bering Sea shelf has a clearly expressed eutrophic structure, corresponding fully to the high productivity of the overlying water. The trophic zonality clearly corresponds to the morphology of the shelf (see Fig. 10a); representatives of all trophic groups have practically 100% occurrence. On the shelf of the East China Sea, over broad areas beneath the low-productivity Kuroshio waters, swallowing detritophages are scarce or absent (Fig. 12), while gatherers are not represented at all stations, the zone of predominance of the leading group (≤50%); over a large area, a zone of dominance of sestonophages is found. If we base our judgments on the distribution of benthic deposits, we would expect the development of three trophic zones and their distribution according to a type typical for broad, flat shelves. Thus, on the shelf of the East China Sea, there is disruption of the trophic zonality, manifested as weak development of the zone of gatherers and total absence of the zone of swallowers over large areas of the shelf. All of this fits the definition of an oligotrophic structure according to M. N. Sokolova.

Fig. 12. Distribution of swallowing detritophages on the shelf of the East China Sea. 1, Swallowing detritophages present in bottom-digger samples; 2, absent.



This similarity is further increased by the agreement of disruptions in the trophic structure with the low-productivity Kuroshio waters.

A similar phenomenon was detected on the shelf of the Great Bay of Australia (Neyman, 1970). This shelf is rather narrow, its main area occupied by a zone of predominance of sestonophages (see Fig. 10c), while the zone of gatherers is shifted to the very edge of the shelf. In terms of morphology and distribution of trophic zones, this shelf is similar to the shelf of western Kamchatka, where the zone of predominance of gatherers is also found at the very edge of the shelf, while the zone of swallowers is shifted to the upper portion of the slope (Neyman, 1969b). However, on the western Kamchatka shelf, with predominance of sestonophages (in places they represent 90% of the total biomass), practically every station brings up significant numbers of gatherers and swallowers, the biomass of which represents 5-10% of the total biomass. In the Great Bay of Australia, gatherers are found at only 60% of stations, swallowers at 25%, while at 40% of stations, neither is found. The Great Bay of Australia, like the East China Sea, contains subtropical waters of low productivity, and here also we see oligotrophic aspects in the structure of the benthos. However, there are no disruptions of trophic zonality here.

We might think that the oligotrophic structure of the benthos would be a general property of the benthos of tropical shelf areas. However, data on the benthos of the shelves of the northern Indian Ocean (Neyman, 1969a) have shown that in areas under productive waters (regardless of the reasons for the increase in productivity), the structure of the benthos is eutrophic, while in areas under lean waters, it is oligotrophic. Data on the benthos of the Bay of Persia (Neyman, Kondritskiy, 1974) do not fit into this scheme--in spite of the high productivity of the waters, the benthos of this bay has oligotrophic features.

Up to now, an oligotrophic benthos structure on shelves has been detected only where the temperature of the water just above the bottom remains above 13°C throughout the year. In cold waters, even with a very short vegetation season (and, consequently, low productivity), as in our own Siberian seas, the benthos has a eutrophic structure (A. P. Kuznetsov, 1970). We should note yet another fact: In contast to the abyssal area, where the oligotrophic structure of the benthos is combined with very low content of organic matter in the bottom deposits (Sokolova, 1969, 1972), on shelves with varying trophic structure of the benthic population, no significant differences have been found in the content of C_{org} in the bottom deposits (Gershanovich et al., 1974).

In the abyssal zone, the oligotrophic structure is combined with deep transformations of organic matter (Bordovskiy, 1964). We did not find analogous data for the shelves. However, since the oligotrophic structure on the shelves was found only with a water temperature which remained above 13°C throughout the year, and since the rate of regeneration of biogenic elements increases by a factor of 10 as the temperature rises from 5 to 30°C (Maksimova, 1974), we can assume that with a high temperature, organic matter unsuitable for the nutrition of detritophages, particularly swallowers, is present in the bottom deposits. It might be thought that the reason for the formation of the oligotrophic structure of the benthos on the shelf is dual--either low productivity of the shelf waters, or very rapid decomposition of organic matter. In either case, the supply of the bottom deposits with organic matter "edible" for detritophagous invertebrates would be reduced, allowing us to retain the term "oligotrophic" for this structure. However, the term does not have the same meaning as in the abyssal zone, either in terms of the reasons of the oligotrophic formation or in terms of the quantitative indices.

We can draw the general conclusion that for shelves in the temperate and cold zones, eutrophic structure is characteristic of the benthos, while in warm waters, depending on the combination of a number of factors, it may be eutrophic or oligotrophic. For example, along the east coasts of the oceans, where zones of constant upwelling of water are found, a benthos with an oligotrophic structure is rare, and is encountered in limited areas. Along the west coasts of the oceans, where the low-productivity central waters approach the coastline quite closely, and in some places even extend onto the shelf, sections with oligotrophic benthos structure are quite common.

As we compare the peculiarities of the benthos of the shelves, which are dependent on the mobility of the water and the particle-size distribution of the bottom deposits, with the peculiarities which depend on the supply of organic matter in the bottom deposits, we detect the following regularities.

1. On shelves with active dynamics of the bottom waters, sestonophages predominate under all conditions. The influence of the production processes and processes of regeneration of organic matter, leading to an oligotrophic structure of the benthos, is hardly noticeable. The trophic zonality characteristic for such shelves under eutrophic conditions is fully retained. Only the occurrence of detritophages, particularly swallowers, changes. They disappear completely from large areas of the shelf.

2. No examples of oligotrophic structure of shelves with weak hydrodynamics have been found.

3. On shelves with spatially heterogeneous dynamics of the bottom waters and eutrophic conditions in the zone of sediment accumulation, zones of predominance of detritophages, swallowers and gatherers are formed. Under oligotrophic conditions, detritophages are weakly developed: In large areas of the bottom they are absent, particularly swallowers. The zone of predominance of swallowers is not expressed, the zone of predominance of gatherers is weakly expressed; throughout almost the entire shelf area, sestonophages predominate. Thus, the disruption of the trophic zonality characteristic of the oligotrophic abyssal zone is seen on the shelves only under conditions of spatial heterogeneity of the dynamics of the bottom waters.

The method of separating trophic groupings on the basis of the source of food has allowed us to approach an interpretation of the connection between the benthic population and the nature of distribution and type of transformation of organic matter, i.e., between the fauna of the benthos and the biogeochemical processes. It has been found that a similar type of transformation of organic matter causes similar development and relationship of trophic groupings under conditions quite different with respect to other characteristics (L. G. Vinogradov, 1963, 1966; Vinogradov, Neyman, 1965). Due to the precise and unambiguous connection with the conditions of sediment accumulation, trophic zones and sets of zones are structural units for the description of planetary regularities of the distribution of the benthic population.

6. Communities of Abyssal Macrofauna. (Z. A. Filatova)

The benthic abyssal communities have not been thoroughly studied. There is a shortage of data on their species composition, geographic area and conditions of habitation. Very little is currently known about the physical and chemical conditions on the bottom and near the bottom, the force and direction of movement of the water above the surface of the bottom. These data, where available, are scattered and largely random. In order to explain the peculiarities of distribution and quantitative predominance of various species of macrofauna on the ocean floor, it is not sufficient to know the depth of the location, the nature and distribution of bottom sediments and the macroscopic bottom relief. We also need information on many other important factors determining the conditions of life in the bottom layer of water and on the bottom itself, as well as how they change with time and space. Nevertheless, using the data which have been accumulated, we can attempt to imagine the composition and structure of abyssal benthic macrofauna biocenoses of the ocean, on the example of the best studied eutrophic zone, that of the northern Pacific. As a first step, let us use the available, though incomplete, data on the specific composition and quantitative nature of the biocenoses, and their distribution over the sea floor.

Deep-water macrobenthic fauna is arbitrarily subdivided into three dimensional groups. The meiofauna (meiobenthos) measures 0.04-1 mm (Thiel, 1966, 1975) or 0.5-5 mm (Sokolova, 1970), and is the most massive group of animals. The macrofauna (measuring 5-10 mm) and megafauna (>1 cm) are the remaining dimensional groups. The nature of the distribution of these groups of animals on the sea floor is related to their dimensions: The smaller the organisms, the more evenly they are distributed on the bottom. Such groups as the small Xenophyophoria, Tanaidacea, Nematoda or the agglutinating Rhizopoda frequently form a sort of continuous "carpet" in a number of regions of the eutrophic zone of the ocean. Therefore, the meiofauna and smaller macrofauna (primarily the megabenthos juveniles) are most completely accounted for by the bottom digger. The larger the organisms, the less evenly they are distributed on the bottom and the more frequently they form various aggregations, "spots" or accumulations. This is a result both of the small-scale peculiarities of distribution of conditions of habitation, and of the nature of breeding and behavior of the larvae and fry.

It is characteristic for deep-water benthic fauna that the species usually have limited geographic distribution, whereas many genera are almost cosmopolitan (Hessler, 1974). This is quite important for the study of the abyssal biocenoses. Studies of the abyssal biocenoses will yield the greatest results where they are most completely developed, i.e., in the eutrophic abyssal zones, e.g., in the North Pacific.

Before turning to an analysis of the biocenoses of the eutrophic North Pacific, let us briefly discuss the peculiarities which distinguish the deep-water (abyssal) biocenoses of the ocean floor from biocenoses of the shelf zone, and analyze the basic aspects of abyssal biocenoses of the eutrophic zone of the ocean.

The tremendous size of the abyssal zone biocenoses is one of their most important specific features. Such factors as depth, bottom relief and composition of bottom sediment change smoothly in the abyssal zone, seasonal and diurnal fluctuations in temperature and salinity are absent, as are tidal movements of the water. Soft sediments predominate, constant currents are slow. In accordance with this, the boundaries of the biocenoses are not sharp, and each biocenosis is large.

A second peculiarity of abyssal biocenoses is the sparsity of macrofauna and megafauna, in spite of the almost continuous distribution of the infaunal meiobenthos in the surface layer of the bottom deposits. This means that the relative quantitative impoverishment of the bottom fauna is great, since the biomass of the meiofauna does not compensate for the low biomass of larger animals. The specific variety of the benthos in the eutrophic zone, however, is rather great.

One peculiarity of the systematic composition of benthic faunal biocenoses of the sea floor might be considered a third peculiarity of abyssal communities. Particularly characteristic are those morphologic features of organisms which are related to the shortage of calcium at great depth, the limited food supply, life in total darkness with very slow movement of the water, in an environment with predominantly soft sediment and high hydrostatic pressure, influencing the rates of growth and metabolism, etc. All of this influences the general appearance of deep water inhabitants; therefore, the abyssal biocenoses differ from shallow-water biocenoses not only in terms of specific composition, but also in terms of the general appearance of the component species.

There are a number of species and genera, less frequently families, which are found only in the abyssal areas, making up the ancient core of the oceanic complex of benthic fauna. These include the glass sponges (Triaxonida), polychaeta from the genera Macellicephala, Macellicephaloides, Kesun, Jasmineira, Maldanella; bivalve mollusks from the genera Malletia, Spinula, Parayoldiella, Ledella, Vesicomya, a number of species of Pennatularia, the sea stars Porcellanasteridae, the Holothurioidea Elpidia, a number of species of the urchins Pourtalesiidae, and many Pogonophora.

Biocenoses of the lower bathyal and abyssal zones, interconnected by gradual transitions with increasing depth, are quite characteristic of the North Pacific. Let us analyze some of these biocenoses, located in the open portion of the Gulf of Alaska and the waters of the North Pacific.

The biocenosis Onuphis pallida-Pavonaria pacifica-Ophiophthalamus normani-Ophiura leptoctenia is found in the upper and middle bathyal region of the Gulf of Alaska. One of its groupings is:

Onuphis pallida-Potamilla symbiotica-Syncoryne sp.-*Ophiophthalamus normani*, which probably extends from the Gulf of Alaska along the island slope of the Aleutians and the eastern coast of Kamchatka to the Sea of Okhotsk. In the Sea of Okhotsk, this is an independent bathyal-abyssal community, extending over depths of 460-3314 m on the slopes of the Academy of Sciences sea mount and in the southern portion of the sea (Ushakov, 1953; Savilov, 1961). In the Gulf of Alaska, it is encountered at depths of 990-1030 m in clayey silt, with a bottom temperature of approximately 3.0°C. The total biomass of the grouping is 5.3 g/m^2. One of the leading forms of this grouping is a clear example of symbiotic adaptation of organisms to life in the soft bottom at great depths. The hydroid *Syncoryne* sp. overgrows the long (up to 50-80 cm) tube of the sedentary polychaete *Potamilla symbiotica*, utilizing it as a substrate, while its hydrorhia creates a thick, circular weave around the lower end of the tube, holding the polychaete in the vertical position (Ushakov, 1950; Tendal, 1971). This represents the "epifauna of the soft bottoms" in its clearest form. For this grouping, the large *Pavonaria pacifica* with *Chondractinia*, many *Spiochaetopterus* polychaetes, *Maldanidae* (up to 160 indiv./m^2, biomass 0.6 g/m^2), *Melinna ochotica*, *Travisia pupa*, etc., are characteristic, of the decapod--juvenile *Chionecetes opilio*, of the bivalve mollusks--the large *Delectopecten randolphi*, the smaller *Nucula cardara*, *Yoldiella derjugini* and others.

The lower bathyal biocenosis *Onuphis pallida-Yoldia beringiana-Ophiura leptoctenia* is found in the Gulf of Alaska at depths of 1050-2088 m, over a rather large region from the east slopes of the Aleutian trough to the traverse of Baranov Island in soft clayey silts; the temperature at the bottom is 1.9-2.0°C. The total biomass of macrofauna is from 0.9-57.8 g/m^2, averaging 13.9 g/m^2. This relatively high biomass of benthic fauna in the lower bathyal is explained by the influence of transport of detritus from the highly productive shelf of the Gulf of Alaska and its accumulation in the lower portion of the slope and in the upper levels of the abyssal gulf (Kuznetsov et al., 1973).

The biocenosis *Onuphis pallida-Yoldia beringiana* is typical for the lower bathyal zone of the Gulf of Alaska. Characteristic for it is the presence of a number of bathyal forms also present in the Bering Sea.

Onuphis pallida is a mass form (100% occurrence, more than 100 individuals in a trawl catch). The large bivalve mollusk *Yoldia beringiana* is quite characteristic for the biocenosis, although it is somewhat less frequently found in trawl catches than *O. pallida* (occurrence 40-50%). This is a typical bathyal form for the northern Pacific Ocean and the far eastern seas. *Ophiura leptoctenia* is also a common form, occurrence about 60%. It is usually distributed in spots, within which its quantity in trawl catches may reach 500-1100 individuals.

One peculiarity of the biocenosis is the presence in its composition of various sea pens (5-6 species, as many as several dozens of individuals in a trawl catch). They are all characteristic for the bathyal and upper abyssal Pacific, surrounding its northern portion in a sort of belt. Particularly common are Pavonaria pacifica (60% occurrence) and Virgularia cystifera (40-50%). The last species, together with Protoptilum orientale, is placed in the group of "coastal deep-water forms" (Pasternak, 1973). The entire set of these Pennatularia, elevated above the surface, is considered part of the "epifauna of soft bottoms."

Of the irregular urchins, abundantly represented in the next biocenosis, here we find only Pourtalesia laguncula beringiana, located in the bathyal of the Sea of Okhotsk and Bering Sea and the northern part of the Pacific Ocean (A. N. Mironov, 1974).

This biocenosis includes both detritus-collecting forms and sestonophages and predators. Characteristic are large Actinia (up to 50 individuals in a catch), the brachiopods Friella halli, the large polychaete Aphrodite talpa, Sternaspis scutata, Terebellide stroemi, Brada irenaia, Samythella neglecta, Travisia forbesi, T. pupa, Augeneria bistriata, etc. Of the small bivalve mollusks, we find Delectopecten randolphi (occurrence about 60%), Nucula tenuis, N. cardara, Dermatomya sp., Myonera garetti (40%), Malletia truncata, M. pacifica, etc. The Echinodermata are represented primarily by a mass of small Ophiuroidea: O. leptoctenia, Ophiophthalamus normani, Ophiolimna bairdi, as well as Holothurioidea from the Stichopodidae and Molpadiidae. The large Echiuroidea Prometor grandis and several species of Pogonophora give this biocenosis an abyssal appearance. It is therefore intermediate in nature between bathyal and abyssal biocenoses in this region.

The biocenosis Ophiura bathybia-Malletia cuneata-Echinocrepis rostrata-Abyssaster tara is encountered in the upper abyssal of the open portion of the Gulf of Alaska, at depths of 2240-4740 m. At depths of about 2000 m, it borders with the above-described biocenosis O. pallida-Y. beringiana.

Probably, the biocenosis O. bathybia-M. cuneata is also located in the adjacent portions of the abyssal northeastern part of the ocean. It is restricted to soft, fine aleuritic and clayey silts, usually with some pebbles and rounded pumice. The bottom temperature is 0.7-1.6°C, averaging 0.9°C. The total biomass of the benthos in the biocenosis is 0.5-3.6 g/m^2, averaging 1.5 g/m^2. This value is characteristic for the northern eutrophic zone of the abyssal Pacific. Large silt-eaters are characteristic for this biocenosis: various irregular urchins and small Ophiuroidea. Small bivalve mollusks frequently form rather large populations. The percentage of occurrence of even the leading forms is low (not over 60%), due to the paucity of macrofauna.

The leading forms are: Ophiura bathybia--dozens or hundreds of individuals in a trawl catch--and Malletia cuneata--in places up to 30-40 individuals.

Of the larger forms, various irregular stars (ten species, up to nine in one station) are important: Echinocrepis rostrata, Cystocrepis setigera, Urechinus loveni, Echinosigra amphora fabrefacta, Aporocidaris fragilis, etc.

Quite characteristic for the abyssal northern Pacific are the sea stars of the family Porcellanasteridae: Eremicaster tenebrarius (up to 15 individuals in a trawl catch), E. pacificus and Abyssaster tara. Among typical representatives of the biocenosis are also Travisia profundi, Sternaspis scutata, Pennatula phosphorea, etc.

The presence of the large Echiuroidea Prometor grandis is characteristic for many regions of the northern (particularly the northwestern) eutrophic portion of the Pacific Ocean; the large proboscis of these animals extends across the surface of the sediment, whereas the Echiuroidea themselves are buried in the soft bottom. In this biocenosis, in addition to P. grandis, we also see the Echiuroidea Ikedella achaeta, the sipunculids--Golfingia capitelliformis and G. birsteini. The polychaetes, usually so numerous, do not form massive settlements here: We can note Travisia pupa, Kesun abyssorum, Onuphis lepta, O. iridescens, etc. Of the bivalve mollusks, Malletia truncata, Myonera garetti, Nucula carlottensis, Delectopecten randolphi, etc., are seen. Four species of "glass" sponges are seen from the genus Hyalonema, as well as other deep-water species of sponge--Cladorhiza longispina, Abyssocladia bruuni, Polymastia sol pacifica, Bathydorus laevis. The spicules of the Hyalonema are inhabited by small Actinia, Ceriantharia, Ascidia, and many Stephanoscyphus. Of the Pennatularia, we find the abyssal species--Umbellula thomsoni and Kophobelemnon stelliferum. Of the Pantopoda we see Hedgpethia articulata and Nymphon procerum. The large Psychropotes and small Myriotrochus and various small Tanaidacea are seen in small quantities.

The large size of the forms included in the biocenosis O. bathybia-M. cuneata, their relatively high population and biomass indicate that the benthic fauna finds good habitation conditions here and that the quantity of food on the bottom can support the development of a varied fauna, particularly collecting and swallowing detritophages.

The biocenosis Spinula oceanica-Eremicaster tenebrarius is purely abyssal, found in the western and central portions of the North Pacific at depths of 4660-6010 m on soft, clayey silts. The macrofauna is still more sparse than in the Gulf of Alaska; in particular, there are almost no irregular sea urchins, the meiobenthos makes up most of the biomass of this biocenosis. The leading forms are the bivalve mollusk S. oceanica, characteristic for the entire abyssal Pacific and eastern Indian Oceans, particularly for the northern eutrophic zone, and the sea star Eremicaster tenebrarius, which, together with E. pacificus, is also typical for the abyssal Pacific Ocean.

The total biomass of the benthos is less than 1 g/m^2, usually 0.10-0.15 g/m^2 (Filatova, Levenshteyn, 1961). These values of biomass are characteristic for the boundary portions of the eutrophic zone of the northern Pacific.

S. oceanica in places forms mass accumulations, up to several dozen individuals in a trawl catch. The similar form S. calcar does not form massive populations. The sea stars E. tenebrarius, E. vicinus, Abyssaster tara, Vitjazaster djakonovi are typical silt-eaters, almost always encountered in numbers of 3-5 individuals per catch. Two or three species of Gorgonaria and Pennatularia, and small individual corals Fungiacyathus symmetricus are characteristic. The small Stephanoscyphus are quite common (up to 15 individuals in a catch, on concretions or sponge spicules), of the sponges--Polymastia sol pacifica, Cladorhiza rectangularis, C. longispina. Of the bivalve mollusks--the small Acar asperula (on spicules of sponges or the beaks of squid), Malletia cuneata, various Ledella and Tindaria, of the polychaeta--Kesun abyssorum, Fauveliopsis challengeria, Maldane harai, etc. The Sipunculids are rather varied--Golfingia vulgaris, G. minuta (up to 120 individuals in a catch), G. improvisa, Phascolion pacificum, Ph. lutense; the Echiuroidea Alomasoma bullata (up to 40 individuals), A. convexa, Ophiura bathybia (up to 235 individuals). Of the irregular urchins, we find only Echinocrepis rostrata.

The numerous meiobenthos consists of small Tanaidacea, Nematoda, Foraminifera (primarily agglutinating), juvenile Polychaeta, bivalve mollusks, Gastropoda, Isopoda, Amphipoda and Ostracoda.

As we move to the south from the relatively productive eutrophic North Pacific and move away from the coast into the open ocean, the composition of the biocenoses gradually changes: The significance of macrofauna decreases, that of meiobenthos increases, and the total biomass decreases. In the vicinity of 30-20°N, the bottom population takes on the form which is usual for the oligotrophic zone of the Pacific Ocean, where the total biomass does not exceed a fraction of a gram per m^2. The remainders of the skeletons of dead macrofauna, nekton and Radiolaria give the bottom population of these regions a characteristic appearance and form a substrate for the sparse epifauna--Stephanoscyphus, small Actinia, etc.

7. Trophic Structure of the Deep-Water Benthos.

(M. N. Sokolova)

The various size-groups of the deep-water bottom population react differently to changes in feeding conditions. Therefore, we should analyze separately the structure of the macrobenthos and meiobenthos. By meiobenthos, we mean invertebrates measuring 0.5-5 mm. (The minimum dimension is determined by the size of the apertures in a No. 140 screen, through which the samples are usually washed, while the maximum is selected arbitrarily.) We consider all organisms larger than 5 mm to be macrobenthos. The meiobenthos makes up the main portion of the samples taken by bottom grabs; the macrobenthos, the main portion of the catch of deep-water trawls. The deep-water macrobenthos is usually absent in the bottom-grab samples (area 0.25 m^2), due to its scarcity, while the meiobenthos is only partially retained in trawl samples.

The majority of the entire deep-water macrobenthos, and particularly of the meiobenthos, falls in the deposit-feeding group (see 3.5), i.e., it feeds on the organic matter contained in the sediment. The invertebrate suspension-feeders consuming suspended (living or dead) organic matter represent a significant portion of the deep-water macrobenthos, but are rare in the meiobenthos. The carnivorous invertebrates, utilizing both living prey and dead animals, are in the minority in the deep-water free-ranging and sessile macrobenthos but, apparently, represent the absolute majority of the nektobenthos. They are in the minority in the meiobenthos.

The trophic structure of the deep-water benthic population, i.e., the quantitative ratio (in our studies--by weight) of invertebrates with various types of feeding experiences significant alterations in the World Ocean in connection with the changes in feeding conditions for the dominant trophic group, i.e., for macrobenthic deposit-feeders. The body sizes of the invertebrate macro- and meiobenthos differ by an average of a factor of 10, which results from the variation in thickness of the sediment layer necessary for maintaining of deposit-feeders of these two size-groups. The requirements of the smaller organisms can be satisfied with a smaller quantity of food, and therefore they can exist in a thinner layer of sediment than can the larger organisms.

On the scale of the World Ocean, the greatest changes in thickness of the surface layer of sediment suitable for feeding of deep-water deposit-feeders are found at the boundaries of the global zones of oceanic sedimentogenesis--in connection with the climatic and circum-continental zonality of sediment formation (Bezrukov, 1962; Lisitsyn, 1974).

In general, in the arid zones only the surface film of sediment is available for the nutrition of deposit-feeders, while in the humid and equatorial zone--a layer of several centimeters is available, and in pericontinental zones of hemipelagic-type sediment accumulation--tens or even hundreds of centimeters of surface sediment are available. The thickness of the surface layer of sediment which can be fed upon by benthic deposit-feeders is greater, with higher rates of sedimentation and greater quantities of organic matter reaching the bottom, to be stored in the sediments in a form which can still be utilized. This layer is thin where sedimentation rates are low and the quantities of organic matter reaching the bottom are minimal, where the organic matter is greatly transformed on the surface of the sediment not being buried (Bordovskiy, 1964, 1966; Romankevich, 1974, 1975). A sharp decrease in the thickness of the layer of sediment suitable for nutrition represents an obstacle to the spreading out of macrobenthic deposit-feeders, more so than for those of meiobenthos. Consequently, most macrobenthic deposit-feeders cannot exist in areas with unfavorable oligotrophic conditions.

Eutrophic conditions are observed in the peripheral and equatorial parts of the Pacific, Indian and Atlantic Oceans with more or less significant rates of accumulation of sediment and organic matter. Oligotrophic conditions are found far from the continents in the open areas of the oceans with low rates of accumulation of sediment and organic matter. The locations of these trophic areas in the oceans are shown in Figs. 13 and 14.

The trophic structure of the macrobenthos changes upon transition from eutrophic areas to oligotrophic areas, whereas the trophic structure of the meiobenthos remains unchanged. In areas with eutrophic conditions, the macrobenthic deposit-feeders are ubiquitous and predominate over large areas of the bottom, except the peaks of underwater sea mounts and areas of erosion on their slopes. In areas with oligotrophic conditions, detritophagous macrobenthos is found rarely or not at all. The macrobenthos in these areas consists of a few immobile suspension-feeders and nektobenthic carnivores (Sokolova, 1964, 1969, 1976; Dayton, Hessler, 1972; Shulenberger, Hessler, 1974). Figures 15 and 16 present examples of the distribution of typical taxonomical groups of macrobenthic deposit- and suspension-feeders in the eutrophic and oligotrophic region of the Pacific Ocean. The total quantity of macrobenthos in the oligotrophic regions is significantly less than in the eutrophic regions (Table 10).

The meiobenthos, both in eutrophic and in oligotrophic regions, consists primarily of detritophagous invertebrates. Upon transition from eutrophic conditions to oligotrophic conditions, the taxonomical composition (Table 11) and biomass of the meiobenthos become somewhat poorer (Sokolova, 1970, see also III.5), but the trophic structure is not altered (Sokolova, 1969, 1970, 1972, 1976).

Due to this, our analysis of the influence of variations in feeding conditions on individual feeding groups and the entire trophic stucture will concern only the macrobenthos.

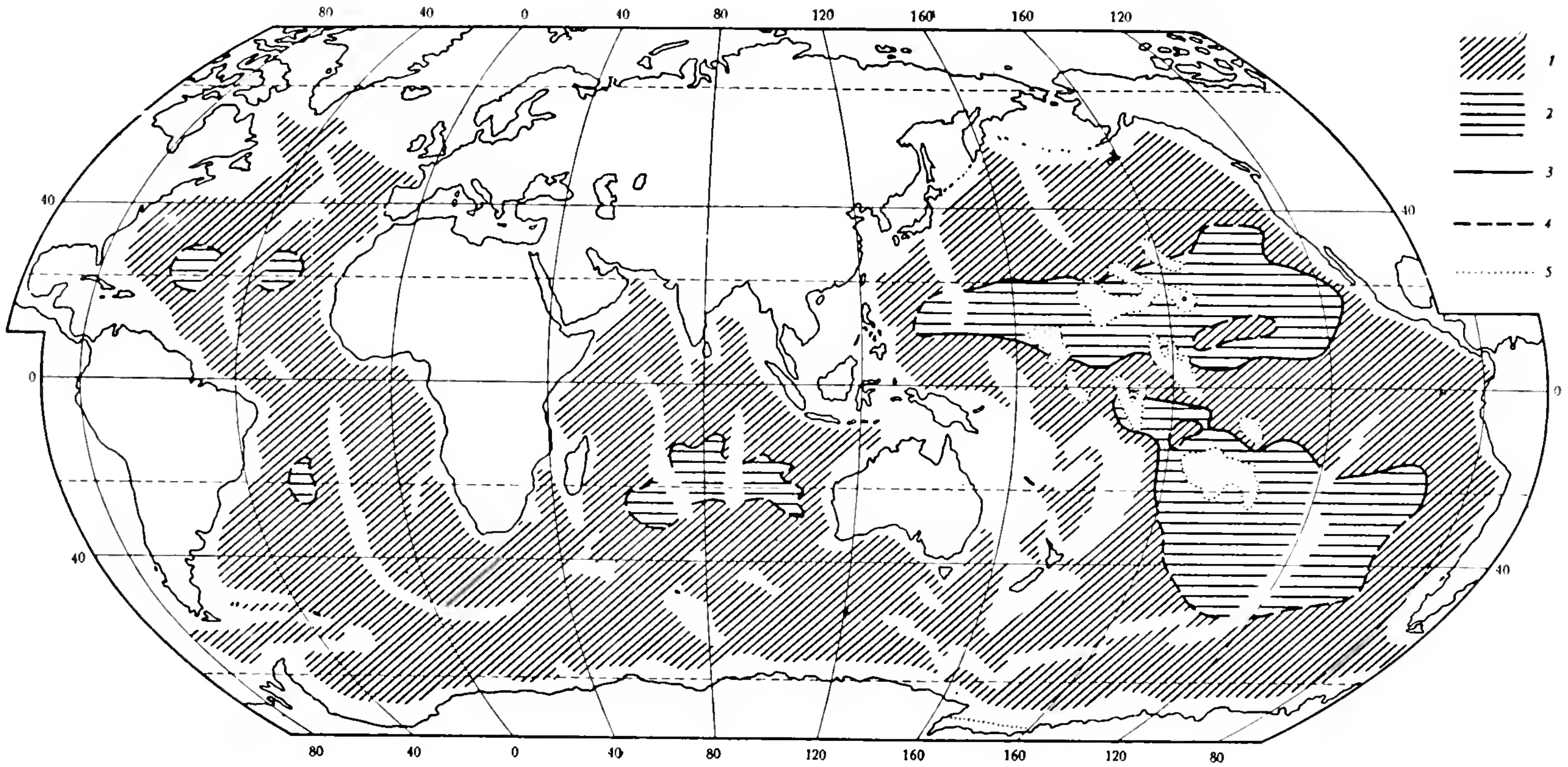


Fig. 13. Deep-water benthic trophic regions at depths of over 3000 m). 1, Eutrophic; 2, Oligotrophic; 3-4, Boundaries between them: based on predominance of deposit-feeders in trawl catches considering the distribution of basic systematic groups of deposit feeders in macrobenthos, weight characteristics of macrobenthos and meiobenthos, as well as conditions of accumulation and predominance of organic matter in the surface layer of the sediment (3); same, but based on less materials (4); 5, Outer boundary of accumulative shelves around islands and underwater sea mounts.

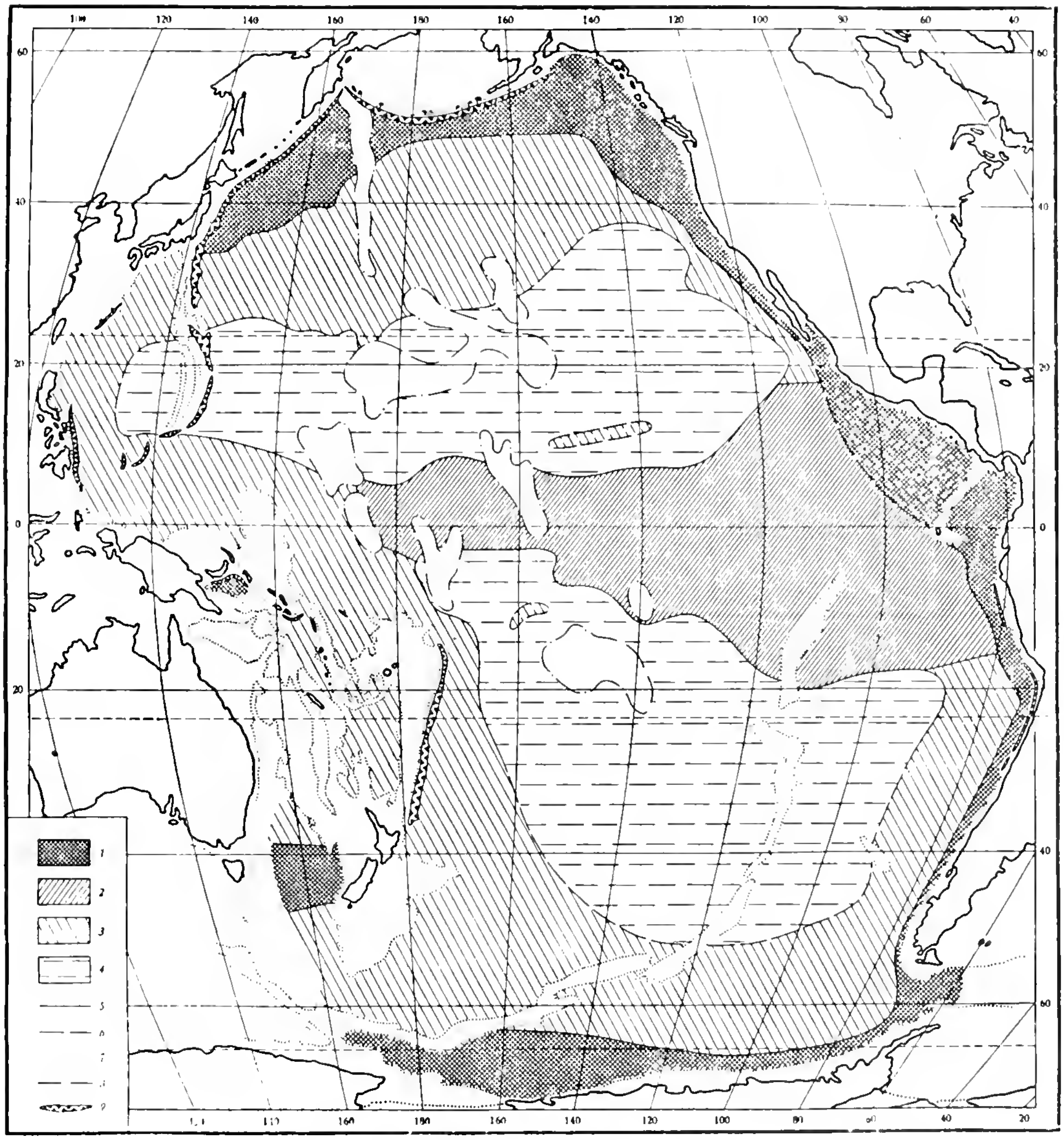


Fig. 14. Diagram of distribution of trophic regions on the Pacific Ocean Floor. Eutrophic regions: 1, Peripheral pericontinental; 2, Peripheral oceanic; 3, Equatorial; 4, Northern and southern oligotrophic regions; 5, 6, Boundaries of regions (symbols same as in Fig. 13); 7, Continental slopes and under-water rises; 8, Outer boundary of accumulative trains (same as in Fig. 13) (not over 300 m deep); 9, Deep-water trenches (over 6000 m deep).

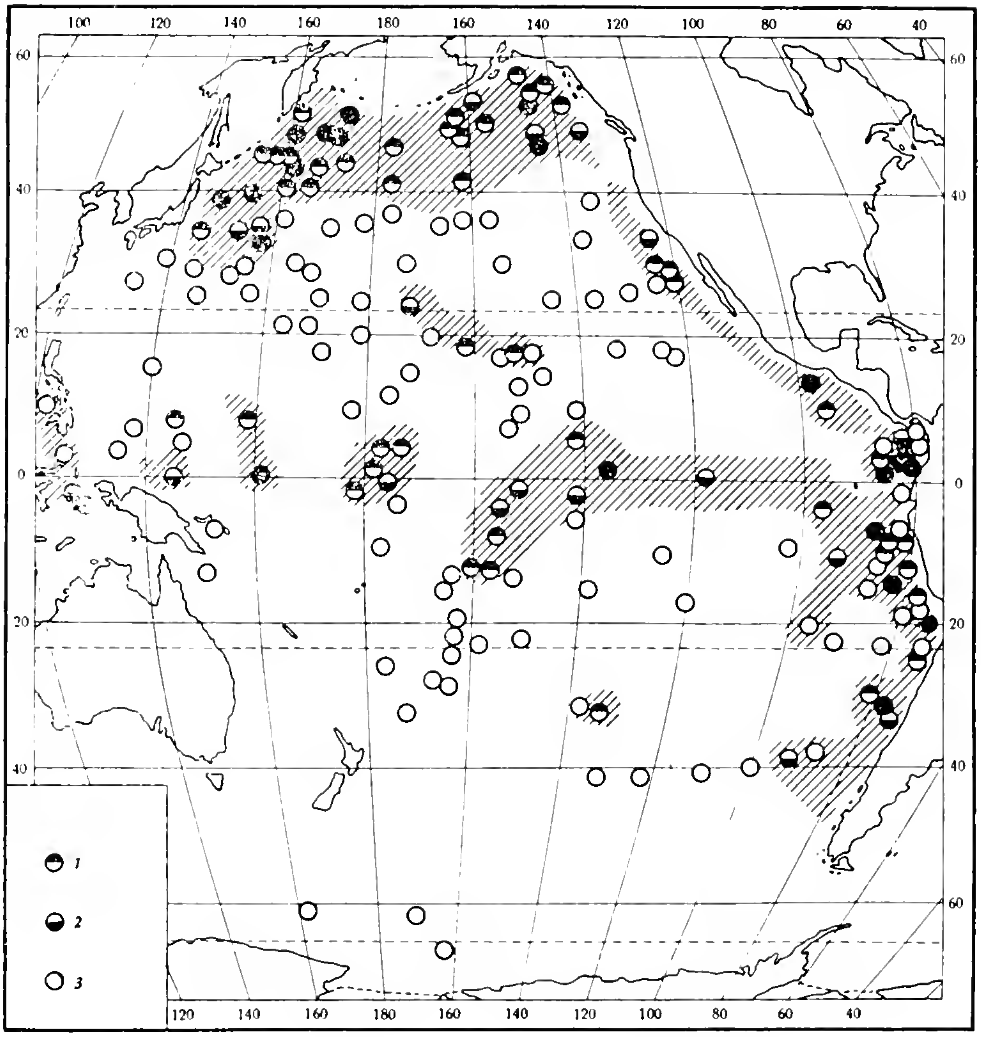


Fig. 15. Diagram of locations of typical groups of deposit-feeders on the floor of the Pacific Ocean. 1, Sea stars of the family Porcellanasteridae: 2, Irregular sea urchins: 3, Neither group present in trawl catches (Sokolova, 1972).

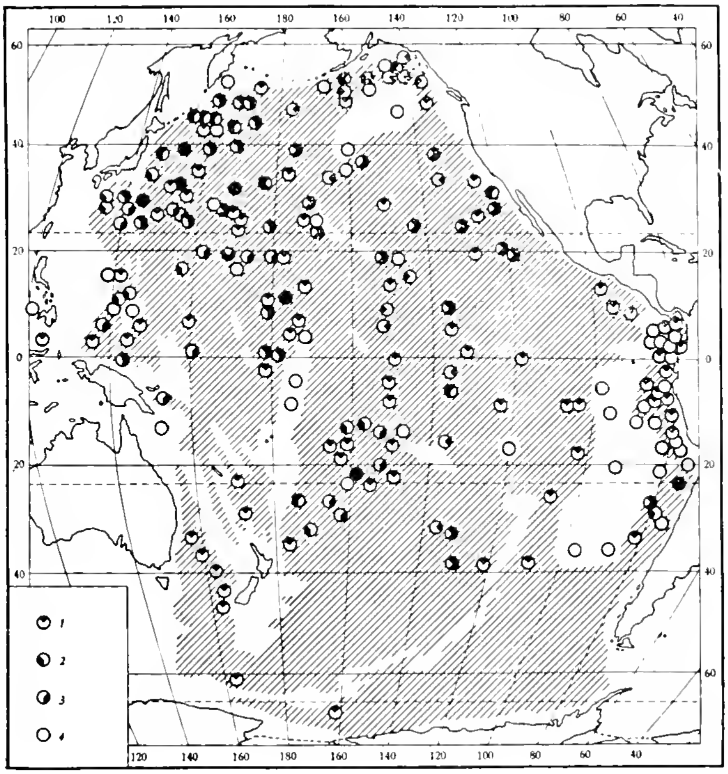


Fig. 16. Patterns of distribution of typical groups of suspension-feeders on the Pacific Ocean floor: 1, sponges; 2, Cirripedia; 3, Polichaeta of family Serpulidae; 4, None of these groups present in trawl catches (Sokolova, 1972).

The boundaries between eutrophic regions divide the areas with similar trophic structure of the population, but with unequally favorable feeding conditions. These differences are sufficient to limit the areas of distribution of certain species of deposit-feeders, which tend toward the boundary separating the eutrophic regions. An example is the boundary of the pericontinental and oceanic peripheral eutrophic regions in the Pacific Ocean (see Fig. 14). Near it, the subsurface reducing zone in the sediment disappears, and the absolute quantity of organic matter buried in the sediment decreases by a factor of 8 (Skornyakova, Murdmaa, 1976). In the macrobenthos, the frequency of occurrence of deposit-feeders decreases--Holothurioidea, sea urchins, stars, Polychaeta, Sipunculoidea, all of which prefer the sediment of the pericontinental eutrophic region (Sokolova, 1976). The species of the genera Travisia and Kesun among the Polychaeta (Levenshteyn, 1970), Cystocrepis, Echinocrepis, Helgocystis and Ceratophysa among the irregular urchins (A. N. Mironov, 1974) do not penetrate into the organic eutrophic region. These and other similar facts explain the rather good agreement of the boundaries between trophic areas and between zoogeographic areas in the abyssal zones (Vinogradova, 1969; Belyayev et al., 1973; Sokolova, 1969, 1972). Obviously, we see here the influence of a sharp change in the feeding conditions on the range of distribution of many species of deep-water benthic invertebrates, most of which are deposit-feeders.

Table 10. Weight characteristics of macrobenthos of eutrophic and oligotrophic regions of the Pacific Ocean floor, based on trawl catches, frame width 2.5 m.

Trophic areas	No. of samples	Weight of microbenthos in trawl catch, g	
		Mean	Range
Eutrophic			
Pericontinental	16	476.83±109.49	1660-38.96
Oceanic	11	28.94± 7.16	71.0- 3.0
Equatorial	5	39.88	140.78-2.45
Oligotrophic			
Northern	7	1.49± 0.39	6.09-0.08
Southern	10	0.39± 0.018	1.06-0.01

Table 11. Frequency of occurrence of basic systematic groups of meiobenthos (%) and mean biomass of meiobenthos in oligotrophic and eutrophic regions of the Pacific Ocean (Sokolova, 1970).

Group	Oligotrophic regions	Eutrophic regions
Spongia	33	60
Nematoda	9	7
Polychaeta (family Serpulidae)	5	27
Polychaeta (detritophagous)	19	20
Isopoda	-	27
Tanaidacea	24	27
Scaphopoda	-	7
Sipunculida	-	7
Bryozoa	14	7
Ascidiacea	-	7
Mean Biomass, g/m^2	0.007±0.002	0.024±0.004
Number of samples	15	12

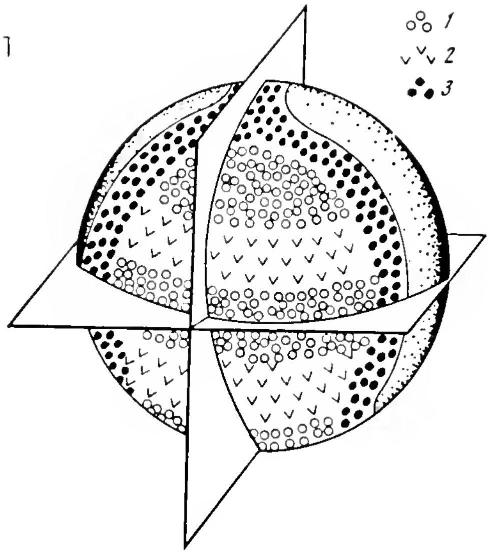
Within the individual trophic regions, we see medium-scale and small-scale changes in feeding conditions, resulting from the influence of bottom topography and hydrodynamics on sedimentation and the content of organic matter in the sediment. These changes lead to unevenness in the distribution of the population of deposit-feeders within the range of distribution of a species.

With various rates of sedimentation, the influence of bottom topography on the redistribution of nutrient material in the sediment varies; where the rates are minimal, the influence is least (due to the paucity of nutrient material). Therefore, in oligotrophic areas the bottom topography is much less important as a factor changing the feeding conditions for the macrobenthos than in the eutrophic areas (Sokolova, 1969). In the eutrophic areas on elevations and protrusions of the sea floor, the quantity of soft sediment usually decreases as a result of slower sedimentation or erosion due to greater mobility of the near-bottom waters (shielding effect); frequently, soft sediments are totally absent. The accumulation of sediments is observed in depressions and on flat bottom surfaces (Lisitsyn, 1974). When the layer of soft sediment is thinned or disappears completely, the macrobenthic suspension-feeders predominate, while deposit-feeders become secondary in importance or disappear. When the sediments accumulate, deposit-feeders predominate. Naturally, changes in the feeding conditions under the influence of bottom topography are less significant than changes with replacement of the eutrophic conditions by oligotrophic conditions.

Within the large-scale forms of bottom topography (continental and island slopes, underwater mountain ranges, basins of the ocean floor), we can observe medium-scale variability of the feeding conditions of the macrobenthos, while within the limits of smaller relief forms (e.g., abyssal hills), we see small-scale changes. These large-, medium-, and small-scale changes in feeding conditions are based on changes in the accessibility of organic matter in the surface layer of sediment, necessary for the nutrition of deposit-feeders, correlated to the thickness of the sediment layer. Under oligotrophic conditions, absence or an insufficiency of food for deposit-feeders, limiting their distribution and preventing their dominance in the macrobenthos, is related to a loss of the nutritive value of organic matter, which is deeply transformed on the surface of the sediment before it is buried, while its supply to the bottom is minimal, sedimentation rates as well as phytoplankton production are lowered. Under eutrophic conditions, absence or insufficiency of food for deposit-feeders is caused by local absence of deposits or erosion of soft sediments and the organic matter they contain when the supply of sedimentary material and organic matter to the bottom is significant and the production of the phytoplankton is high.

The concept of the trophic zone, which we introduced (see III.5), allows us to characterize the trophic structure of the deep-water macrobenthos in various scales. The medium-scale zonality refers to the distribution of feeding groups within the limits of the main large forms of bottom topography, while the small-scale zonality refers to the limits of medium and smaller forms of relief. Within the limits of the

Fig. 17. Large-scale trophic zones of deep-water macrobenthos. 1, Latitudinal eutrophic zones; 2, Latitudinal oligotrophic zones; 3, Pericontinental eutrophic zone.



large relief forms, as the sedimentation conditions change with depth, regular alternation of zones of predominance of deposit- and suspension-feeders is observed, i.e., vertical trophic zonality in the distribution of feeding groups. In the deep-water macrobenthos, this zonality is most clearly seen on the slopes of the continents and trenches. The zones of deposit-feeders here are much larger and more regular than the zones of suspension-feeders. With the transition from the slopes to the bottom of the trenches, the vertical trophic zonality, under the influence of relief, is replaced by a patchy distribution of feeding groups (Sokolova, 1960, 1964, 1969).

The global trophic zonality of distribution of deep-water macrobenthos is determined by the distribution of the main productive zones in the ocean. Two types of zonality are distinguished: latitudinal (climatic) and circumcontinental. The combination of these two types of zonality defines the existence of eutrophic and oligotrophic regions on the ocean floor (see Fig. 13). The latitudinal trophic zonality of the deep-water macrobenthos consists in an alternation of gigantic zones of predominance of detritophagous invertebrates and sestonophagous invertebrates from north to south (Fig. 17). These zones agree approximately with the climatic zones of sedimentogenesis in the ocean (Lisitsyn, 1974). The two temperate, and humid equatorial zones of sedimentogenesis generally correspond to the eutrophic zones of deposit-feeders, the two arid zones--to the northern and southern oligotrophic zones of suspension-feeders.

The circumcontinental zonality of distribution of feeding groups of the deep-water macrobenthos consists in the existence of large-scale eutrophic zones of predominance of deposit-feeders in the pericontinental portions of each ocean. The deep-water eutrophic pericontinental zones of deposit-feeders occupy the continental and island slopes, the deep-water trenches and the boundary portion of the ocean floor at the bases of the slopes. The pericontinental eutrophic zone of deposit-feeders is superimposed on the latitudinal trophic zones and enriches the pericontinental portion of the latitudinal oligotrophic zones of suspension-feeders, located near the center of the ocean.

CHAPTER IV. PRODUCTION OF MARINE COMMUNITIES

1. Primary Production. (O. Y. Koblentz-Mishke, V. I. Vedernikov)

The subject of this section is the primary production of organic matter in the ocean. It is usually identified with the photosynthesis of algae, primarily planktonic algae. Actually, primary production should be identified not only with photosynthesis, but also with all primary biosynthesis, which consists of photosynthesis and mineral nutrition. The heterotrophic feeding of phytoplankton, although it increases the same biomass which is formed in the process of primary production is, strictly speaking, secondary production. The same applies also to the heterotrophic feeding of bacteria and to almost all forms of chemosynthesis, since the source of energy in chemosynthesis generally consists of the organic compounds or products of their decomposition, produced earlier in the process of photosynthesis. In other words, the energy stored in these substances in the form of chemical bonds is transformed solar energy, absorbed in the process of photosynthesis.

The study of the primary production of the World Ocean was begun in the 1920's by the oxygen method, which is not highly sensitive. Some estimates of the total value of primary production in the marginal seas were produced by the method of the balance of nutrients. Extensive development of the study of primary production began in 1951, when E. Steemann Nielsen introduced the radiocarbon method of its measurement. For some time, until approximately 1960, intensive collection of data by routine methods predominated. This descriptive stage was consummated by the composition of a map of primary production (see Biologiya okeana. Biologicheskaya struktura okeana [Ocean Biology. The Biologic Structure of the Ocean]). In the last 15 years, works on physiologic interpretation of the measured values have predominated, resulting in some decrease in further collection of large quantities of data. The physiologic approach to the problems of primary production has resulted in the use of various, basically biochemical indices and the revision of the radiocarbon method. At the present time, we see a gap in the "meeting point" of the results of physiologic works, which in most cases are performed using cultures of algae, and the results of field observations. The data produced from cultures are frequently simply transferred to natural conditions without reservation, although in many cases there is no sufficient basis for this. In this section, in order to establish the relationships between the level of primary production, structural characteristics of phytoplankton and conditions of its existence, we shall utilize materials obtained under conditions as close as possible to natural ones. Particular attention shall be given to a differentiated approach to results obtained in the various regions of the World Ocean. Comparisons have been made separately for the polar, temperate, and tropical zones and for the oligotrophic, mesotrophic, and eutrophic communities with primary productions of <100, 100-500, and >500 mg C/m^2 per day. Sometimes mesotrophic waters are divided into three types with primary productions of 100-150, 150-250, and 250-500 mg C/m^2 per day. Data for each type of water vary significantly. This spread of data is caused both by natural fluctuations and by methodologic errors, particularly biologic errors.

1.1 Methodologic Problems

Let us now discuss methods of measurement of the parameters of primary production, which have significant influence on the factors which we shall analyze below. Errors in biologic measurements--of photosynthesis, concentrations of chlorophyll, and quantities of phytoplankton--are 1 or 2 orders of magnitude greater than the errors in measurement of chemical and physical quantities. Furthermore, different authors use different modifications of methods of biologic measurements, whereas the physical and chemical methods used are generally standardized.

Primary Production. As a result of many methodologic studies, it has become clear that the radiocarbon method, in the form in which it has been used to date, measures the increase only in the biomass of phytoplankton, as a result of autotrophic fixation of CO_2. Dissolved organic matter, synthesized by algae, and the increase in biomass of phytoplankton resulting from heterotrophic nutrition, are not measured. The results produced by this method are closer to net production than to gross production, particularly when there is a nutrient limitation (Ketchum et al., 1958).

In determining primary production, a distinction must be made between measurement techniques, on the one hand, i.e., chemical and radiochemical approaches to the measurement of the rate of photosynthesis (production) in each individual sample and the corrections which have been introduced to the final results, and on the other hand, the plan of measurement, i.e., the conditions of exposure of samples and the system of calculations used to consider changes in production with depth. The simplest and most natural method is the plan of experiments in situ. Unfortunately, under the complex conditions of oceanographic expeditions, it is frequently impossible to perform such measurements. Therefore, a number of plans have been suggested to allow the measurement of primary production in the water column without performing investigations. The first was suggested by Steemann Nielsen (1952): the measurement of photosynthesis in samples taken from various depths and incubated under conditions of standard illumination. The second plan, suggested by Yu. I. Sorokin (1956), is based on the measurement of photosynthesis of phytoplankton in a sample of water from the surface of the sea, with subsequent introduction of corrections for changes in its rate with depth. These corrections reflect the unevenness of vertical distribution of phytoplankton, as well as the change in the quantity of light energy, necessary for photosynthesis, with depth, and are determined experimentally. A third plan, which has become most widely used in recent times, consists in the measurement of the intensity of photosynthesis in samples brought up from various depths under conditions of natural illumination, reduced by neutral or selective (blue) filters. The degree of attenuation of light corresponds to its attenuation in the sea at the depth at which the samples were taken (samples taken from the surface were exposed to natural illumination). A fourth plan for determination of primary production is the "chlorophyll" method of Ryther and Yentsch, and is essentially the same as the plan of Sorokin. The heterogeneity of the vertical distribution of phytoplankton is considered by determining the concentration of chlorophyll, while the correction for light is introduced using the curve of variation of photosynthesis with light intensity. The relationship of photosynthesis to concentration of chlorophyll with optimal illumination (AN_{opt}) is assumed constant.

All of these plans, naturally, are imperfect. Measurements in situ most closely reflect the phenomena which occur in nature, and can be used as a standard.

A distinction can be made between random and systematic errors for the various techniques of measurement. Random errors, based on the results of the 52nd voyage of the VITYAZ', amounted to about 20% of the total deviations of data, resulting from errors in methods and the natural fluctuations. The relative total deviations increase exponentially with decreasing production (Fig. 1). With a production of 0.1 mg C/m^3 per day, the total deviation is 100%; this value may be considered the limit of sensitivity of the method (Koblentz-Mishke, 1961).

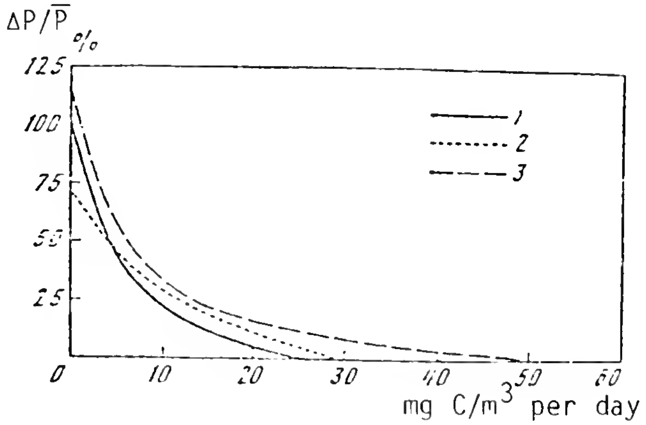


Fig. 1. Relative deviations (%) of primary production (P) at the surface, based on data from the 29th voyage of the VITYAZ' (1), the 46th voyage of the HUGH SMITH (2) and the 46th voyage of the OSHORO-MARU (3).

Of all the systematic errors of the radiocarbon method, the most important are errors in determination of the stock activity of the solution and in filtration. Differences in methods of determination of the stock activity are particularly significant when window-type counters are used, amounting to 10-20% or even 30% (Jitts, Scott, 1961; Sorokin, 1963; Steemann Nielsen, 1965). Recently, most researchers have begun using scintillators; therefore, this source of error has become less significant.

The basic criticism of the radiocarbon method concerns the loss of a portion of the synthesized organic matter by filtration, acid treatment, storage, and drying of filters. Filtration causes a loss of dissolved assimilates and organic matter formed by Flagellata and other algae which pass through the filters either whole or in damaged form, acid treatment results in loss of easily hydrolyzed carbohydrates, while drying and storage results in loss of volatile compounds such as volatile acids and ketones. Most numerous are works dedicated to the losses of dissolved organic matter by filtration. After summarizing the data of a number of authors, we have come to the conclusion that these losses, in the surface layer and throughout the entire euphotic layer, are usually as follows: with primary production of <150 mg Cm^2 per day--5-50%; with production of 150-250 mg C/m^2 per day--5-30%; at 250-500 mg C/m^2 per day--20%, at >500 mg C/m^2 per day--≤10%.

Pigments. In addition to the primary production determinations, productivity is frequently evaluated using the data on quantity of nutrient salts, phytoplankton, the content of suspended matter, ATP or photosynthetic pigments. The later (usually chlorophyll *a*) is particularly frequently used. At the present time, a quantitative relationship has been obtained between the concentration of chlorophyll and primary production. It is still more important to note that the content of pigments allows us to relate the results of determination of photosynthesis to their quantity, and thus perform the physiological analysis of the production process.

Determination of pigments in a sample of sea water can be conducted chromatographically, fluorometrically, or by standard spectrophotometric methods, the latter being used in most investigations. Its principle were developed by Richards and Thompson (1952), then further improved (Parson, Strickland, 1963; SCOR UNESCO, 1966). A comparison of the data obtained using the formulas of Richards and Thompson (taken as unity) and derived on the basis of the new specific coefficients of extinction of chlorophylls, the equations of SCOR UNESCO, and Parsons and Strickland is presented below.

Author	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *c*
Richards, Thompson, 1952	1.00	1.00	1.00
Parsons, Strickland, 1963	0.76	1.05	0.57
SCOR UNESCO, 1966	0.74	1.36	0.53

Systematic errors of determination of pigments are also based on incomplete collection of plant material by filtration. In particular, some of the chlorophyll *a* and its derivates pass through the No. 5 membrane filters used in the USSR (Koblentz-Mishke, Konovalov, 1974). The magnitude of this error has never been estimated, but it is probably not great, since the filters used by specialists of different countries produce practically identical results, although their pore diameters are significantly different (SCOR UNESCO, 1966).

In the lower layers of the euphotic zone, one serious source of systematic errors, leading to overestimation of the results of determination of the content of photosynthetically active pigments, may be the presence in samples of products of the transformation of these pigments. Upon loss of the central Mg atom, chlorophyll is converted to phaeophytin, upon loss of phytol--to chlorophyllide and upon loss of phytol and Mg--to phaeophorbide. The absorption spectra in extracts practically coincide for chlorophyll *a* and chlorophyllide *a* and also for phaeophytin *a* and phaeophorbide *a* (Holt, Jacobs, 1954; Strickland, 1965; Lorenzen, 1967); therefore, standard spectrophotometric methods can determine only the sum of chlorophyll plus chlorophyllide. If a sample contains phaeophytin *a* or phaeophorbide *a*, calculations by the standard equations will lead to the overestimation of chlorophyll *a* by a quantity equal to 59% of the content of phaeopigments. Recording of the spectrum of an extract after acidification (Lorenzen, 1967) allows a correction to be introduced for the content of phaeopigments but cannot allow separate determination of chlorophyll and chlorophyllide.

Random errors in the determination of pigments, using the standard spectrophotometric method, consist basically of errors in the reading of transmission or extinction spectra.

With the identical concentration of pigments, the accuracy of determination of chlorophyll *a* is 2-3 times greater than that of chlorophyll *b* and 4-6 times greater than that of chlorophyll *c*. The shortcomings of the standard method lead in many cases to great errors in the determination of the content of chlorophyll *b* and chlorophyll *c* in phytoplankton (Strickland, Parsons, 1965; Madgwick, 1966; Wauthy, Le Bourhis, 1966; Pyrina, Yelizarova, 1971).

Chlorophyll *a* is the only pigment which is determined with sufficient reliability by the standard method. If the samples contain no products of decomposition of chlorophyll *a*, parallel measurements of its content by chromatographic and spectrophotometric methods yield identical results (Madgwick, 1966). The systematic errors in determination of chlorophyll *a* by the fluorometric and spectrophotometric methods usually lead to overestimation of the results (if phaeopigments are not determined). The relative random error of determination of this pigment, as of primary production, increase with a decrease in its concentration.

Phytoplankton. Data on phytoplankton are required for physiologic interpretation of the results of determination of primary production. Of particular significance are data on the biomass (B) of phytoplankton, expressed as primary production in mg C/m^3 (C_{phyt}). At the present time, three methods are used for determination of phytoplankton carbon: the indirect methods based on ATP (Holm-Hansen, Booth, 1966) and chlorophyll (Vinberg, 1960; Strickland, 1960), and the direct method based on microscopic counting of phytoplankton cells and measurement of their volume, with conversion by equations (Mullin et al., 1966; Strathmann, 1967). All three methods are based on coefficients obtained in cultures. For the conversion from ATP to C_{phyt}, a single coefficient of 250 is used, regardless of the ecologic conditions (Holm-Hansen, 1969), while the conversion from chlorophyll to C_{phyt} uses the coefficient 30 for cultures and nutrient saturated phytoplankton and coefficient 60 for light-inhibited and nutrient-deficient phytoplankton (Strickland, 1960). Obviously, the failure to use differential coefficients for different ecologic conditions must lead to variations in the results of the application of these two methods of estimation of C_{phyt}. One shortcoming of the third method is its frequent and significant undercounting of the number of cells and biomass of phytoplankton as a result of losses of fragile forms.

1.2 Comparison of Results of Determination of Parameters of Primary Production at the Surface of the Ocean.

In order to estimate the contribution of systematic errors of the methods outlined above to ecologic calculations, we have determined the most probable correlations of production (P), chlorophyll (Cl) and cell number of phytoplankton (N) in pairs for the eutrophic, mesotrophic and oligotrophic stations (Fig. 2). The best agreement was produced for the production-phytoplankton relationships. The differences in other relationships fall within the limits of the standard deviations. The similar course of the curves obtained directly and calculated on the basis of the results of two other relationships indicate that the material used was sufficiently representative.

Conversion coefficients from N to B of phytoplankton (Fig. 3) and C_{phyt} were derived on the basis of a large quantity of material. For approximate estimates, one can assume that 1 mg of carbon is contained in 2 million cells of phytoplankton--the average for various regions of the World Ocean during various seasons of the year (Koblentz-Mishke, Vedernikov, 1973). Using these relationships, we can approximately estimate the specific production (P/B), and, using the equation $n = \log(P/B + 1)/\log 2$, we can calculate the rate of cell division n (assuming that each cell division results in a doubling of the content of carbon in the daughter cells). Based on the same graphs, we can calculate the mean content of chlorophyll in the cells of phytoplankton (Cl/N) and in the biomass (Cl/C_{phyt}), the assimilation of carbon by one cell (P/N), as well as the daily assimilation number (DAN), separately for the oligotrophic, mesotrophic and eutrophic zones of water (Table 1, Fig. 4). The indices which are calculated without using the quantity of phytoplankton agree rather well with the data from the literature, particularly for the mesotrophic and eutrophic waters. Corrections for possible systematic errors in the determination of primary production and chlorophyll have little influence on the equations produced. The situation is different with the equations which include data on cell count and biomass of phytoplankton, and on the content of carbon in the phytoplankton. Authors who have determined C_{phyt} by various methods

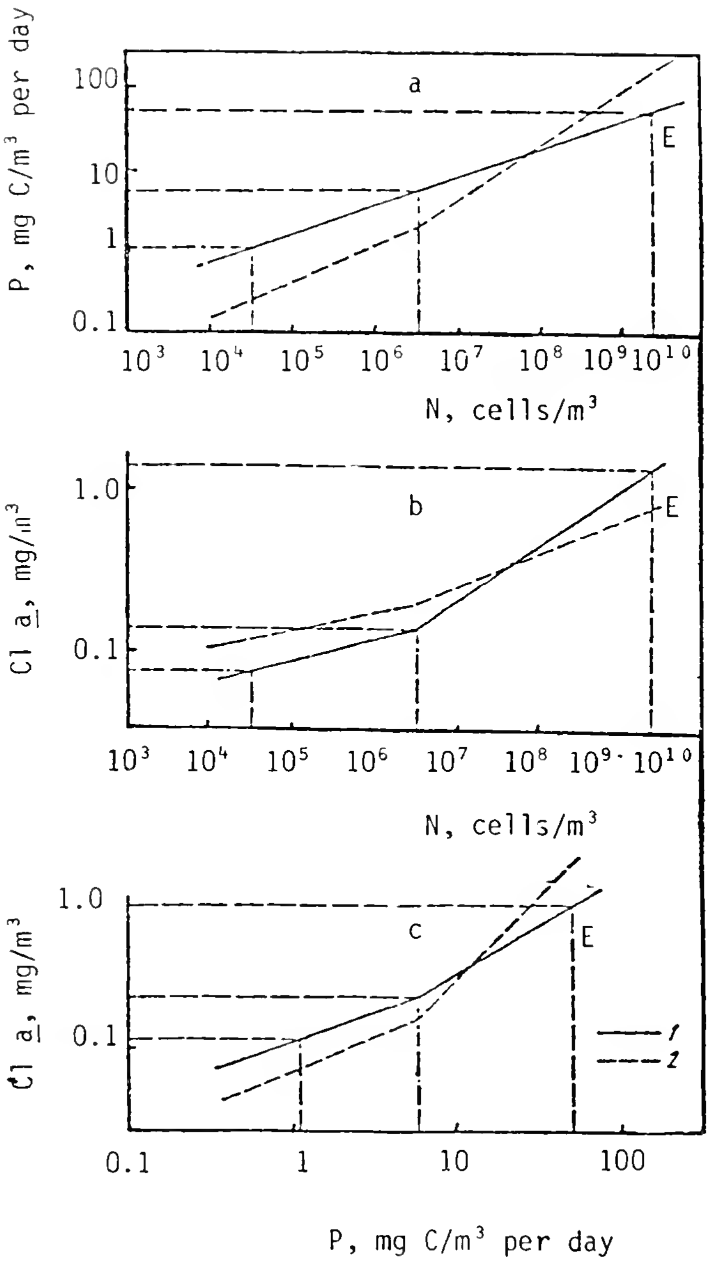


Fig. 2. Relationships of parameters of primary production at the surface of the ocean (after B. V. Konavalov): a, primary production (P) and cell count of phytoplankton (N); b, chlorophyll a (Cl a) and N; c, Cl a and P; 1, regression line produced by direct comparison; 2, regression line produced by applying the results of two different graphs; O, oligotrophic waters; M, merotrophic waters; E, eutrophic waters.

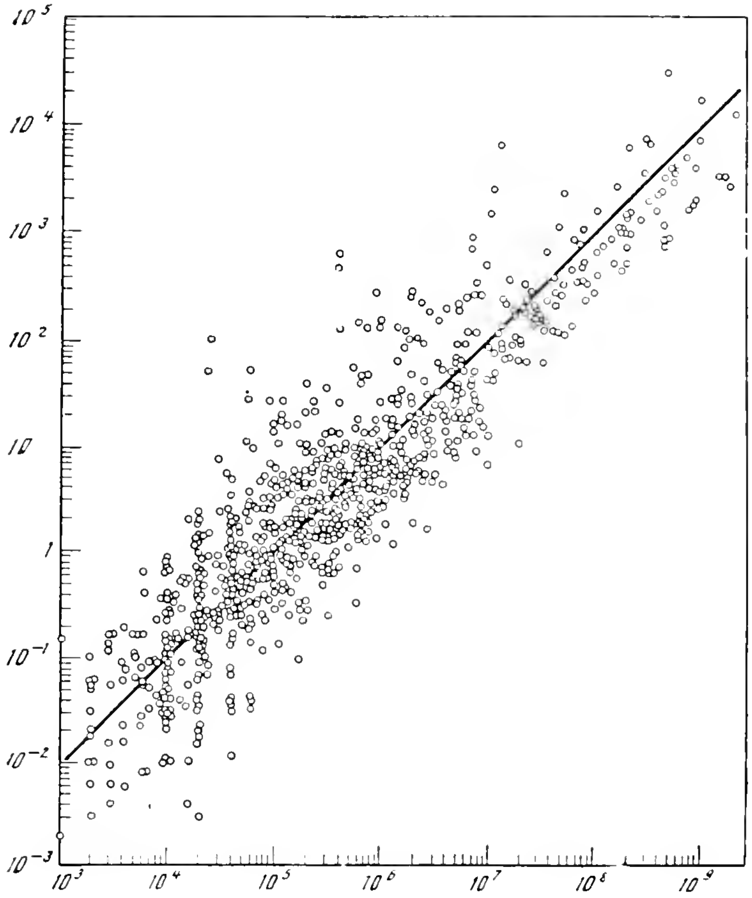


Fig. 3. Number of cells per m^3 (abscissa) and biomass (mg/m^3, ordinate) of phytoplankton from the Pacific, Indian and Atlantic Oceans.

have obtained rather similar results for the eutrophic and mesotrophic zones, but greatly differing results for the oligotrophic zones. Based on the results of direct determination of C_{phyt} in oligotrophic waters, the rate of cell division and content of chlorophyll in them is higher than in mesotrophic and eutrophic waters, whereas calculations based on ATP and chlorophyll lead to the opposite conclusion. Direct microscopic determination of C_{phyt} produces paradoxical results. Whereas it can be assumed that in oligotrophic waters, the cells divide an average of 6 times per day (Koblentz-Mishke, Vedernikov, 1973), it cannot be true that C_{phyt}/Cl is equal to 0.07 here, i.e., that the cells of the algae contain 15 times as much chlorophyll as carbon. Even if the phytoplankton consisted of chlorophyll alone, this ratio would be approximately 0.7. In actuality, we can assume that it is at least $\geqslant 4$ (Steele, 1959; Strickland, 1967). Considering that the overestimation of the concentration of chlorophyll in the oligotrophic waters could hardly be over 50%, we must assume that C_{phyt} is undervalued by the counting method by a factor of at least 50 in this case. This apparently results from underestimation of amount of Flagellata, Coccoliths and other nanno-forms. These forms, of course, are also lost during collection and treatment of richer samples, but they represent a smaller fraction of the cell counts and biomass of the phytoplankton (Sukhanova, in print; Beers et al., 1975).

The introduction of corrections yields more realistic but also questionable coefficients (see Table 1).

Table 1. Relationship between basic characteristics of phytoplankton and its production at the surface.

Item	Oligotrophic Water	Mesotrophic Water	Eutrophic Water
Production P, mg C/m^3 • day	$\frac{1(1.5)}{<0.1-10}$	$\frac{10(11)}{<0.1-100}$	$\frac{50}{1-100}$
Cell count, N cells/m^3	$\frac{2 \cdot 10^4}{2 \cdot 10^3-10^5}$	$\frac{5 \cdot 10^6}{10^6-10^7}$	$\frac{10^9}{10^8-10^{10}}$
Biomass C_{phyt}, mg C/m^3	$\frac{0.01(0.5)}{0.001-0.05}$	$\frac{2.5(5)}{0.5-5}$	$\frac{500}{50-5000}$
Cl, mg/m^3	$\frac{0.15(0.075)}{0.09-0.21}$	$\frac{0.25(0.22)}{0.15-0.35}$	$\frac{5.5}{2.5-8.5}$
P/C_{phyt}	$\frac{100(3)}{<100-200}$	$\frac{4(2.2)}{0.2-20}$	$\frac{0.1}{0.02-0.2}$
P/N	$5 \cdot 10^{-5}$	$2 \cdot 10^{-6}$	$0.5 \cdot 10^{-7}$
DAN = P/Cl	7(20)	40(50)	9
Cl/N	7.5•10-6	$0.5 \cdot 10^{-7}$	$0.5 \cdot 10^{-8}$
Cl/C_{phyt}	15(0.15)	0.1(0.045)	0.011
C_{phyt}/Cl	0.07(6.7)	10(23)	90

NOTE: Numerators show mean values (in parentheses with approximate corrections for systematic errors); denominators show limits of variation.

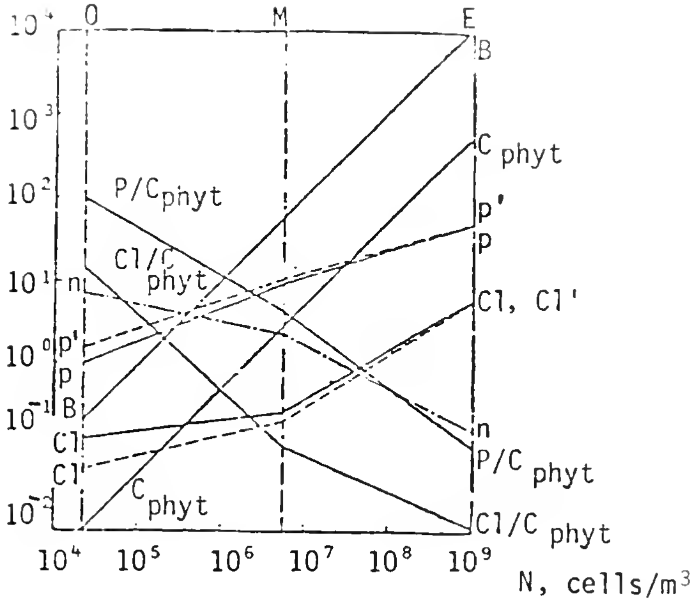


Fig. 4. Comparison of mean values of parameters of productivity and their relationships for oligotrophic (O), mesotrophic (M), and eutrophic (E) surface waters of the World Ocean with cell count, N (cells/m^3); B, raw biomass; C_{phyt}, biomass expressed as carbon; P, primary production; P', same, with correction for maximum possible systematic error; Cl, concentration of chlorophyll a; Cl', same, with correction; n, number of divisions per day.

1.3 Environmental Factors Influencing Primary Production

The combination of results obtained in experiments with individual organisms does not explain fully the occurrence of processes in communities, since complication of the biologic structure leads to the appearance of additional properties. Therefore, the basic equations for primary production as a function of environmental factors must be derived from the results of observations at sea.

Conditions of illumination. Of the factors influencing primary production in the ocean, the intensity of underwater illumination as a reason for the variation in photosynthesis has been most thoroughly studied. Light curves of photosynthesis are constructed for quantitative description of this variation. Usually, samples from different levels are exposed under different conditions of illumination (at sea or in incubators) with parallel determination of the concentration of chlorophyll. The data produced are used to construct light curves of the assimilation number (AN). Another method is based on exposure of aliquots of one sample to various light conditions.

The light curves of AN are usually approximated by the formula of Steele (1962); the position of the optimums on these curves differs somewhat depending on the method of measurement used (Kabanova et al., 1964). The most representative are curves of the assimilation number obtained in situ, the least representative are the results of measurement in incubators with neutral filters, since the spectral composition of the light which penetrates these filters differs significantly from the spectral composition of the radiation which penetrates the sea. The optimal illumination (in the photosynthetically active radiation [PhAR] range) for photosynthesis of phytoplankton in the upper layers of the euphotic zone in most cases is 0.03-0.15 cal/cm^2·10^3 lux (Mandelli et al., 1970; Burkholder et al., 1967). The absence of light depression under these conditions can be explained to a significant extent by the good conditions of mineral nutrition and (or) the dominance of dinoflagellates, which are more resistant to strong irradiation than are the diatoms, as well as the presence of large quantities of yellow organic matter, absorbing ultraviolet radiation. In addition to populations which are resistant to light, populations have also been found, the photosynthesis of which reaches a maximum at very low values of irradiation: 0.003-0.015 cal/cm^2·min, or 2-10 cal/cm^2·day (Koblentz-Mishke et al., 1970; Vedernikov, Solov'yeva, 1972). These value of saturating intensity of light were obtained on foggy or cloudy days.

The phenomenon of light adaption has been extensively studied in cultures of algae. As in these cultures, the cells of planktonic algae, adapted to intensive light and placed to the conditions of saturating light, manifest higher values of AN than do "shade" cells. It is well known that the light curves of photosynthesis of phytoplankton living at various depths differ in terms of the position of the optimums: for surface phytoplankton, they correspond to higher levels of irradiation than for deep-water phytoplankton. The difference depends on the degree of stratification of the water, i.e., the time of adaptation of algae to specific conditions of illumination.

In a number of regions of the World Ocean, a direct relationship has been noted between the incident irradiation and irradiation for which the maximum values of AN are observed. This relationship was detected in July-August of 1966 over the Kuril-Kamchatka trench in the Pacific Ocean (Koblentz-Mishke et al., 1970). It has been shown that the higher the irradiation at a given station, the higher the value of irradiation which corresponds to the optimum on the light curve of AN, determined by experiments in situ. Analogous results were obtained on expeditions of the Institute of Oceanography, USSr Academy of Sciences, in the southwestern Atlantic and southeastern Pacific (Vedernikov, Starodubtsev, 1971; Kabanova et al., 1974a,b). In the littoral waters of the Barents Sea in the summer of 1967 a parallel was observed between incident radiation and the position of the light optimum of the AN (Vedernikov, Solov'yeva, 1972). The variation found in the Barents Sea manifests seasonal adaptation, appearing as a sharp drop in the light optimum in the fall, and a less clearly expressed rapidly occurring adaptation for cultures and natural populations of marine phytoplankton (Steemann Nielsen, Hansen, 1959; Menzel, Ryther, 1961b; Ichimura, Aruga, 1964; Krupatkina, 1970). The latter type of adaptation is probably similar to the examples presented above of light adaptation in the Pacific and Atlantic Oceans. This phenomenon has not been observed for marine waters, but has been observed in Lake Erie (Verduin, 1956). The maximum of photosynthesis of phytoplankton in this lake is observed during the various seasons on sunny days at higher levels of irradiation than is the case on cloudy days.

Thus, many reported facts indicate that the position of the light optimum for photosynthesis is related to the conditions of illumination at the moment of measurement. In contradiction to this, some authors (Finenko, in print; Aruga, 1965) believe that the light optimum of photosynthesis of phytoplankton depends primarily on temperature. To check the correctness of these hypotheses using a single mehod (Yerlov, 1970), data were processed from 77 stations from both domestic and foreign expeditions, in which the measurements of photosynthesis *in situ* were accompanied by optical observations. The values of the light optima were taken from the light curves of AN obtained at these stations. They were related to the incident radiation on the date of measurement (Fig. 5a) and to the temperature at the depth of the optimum (Fig. 5b). We can see that the position of the optima depends to a greater extent on incident radiation than on temperature. Thus, the assumption of rapid alteration of the light optimum for photosynthesis as a function of weather conditions is confirmed. It is possible that this alteration is related not so much to adaptation of the phytoplankton to the level of irradiation present as to the different depths of penetration of the near ultraviolet, deactivating pigments, and other peculiarities of the light field. This would explain why, in highly eutrophic waters, with significant quantities of impurities, the light optimum for photosynthesis is found at the surface under conditions of much more intensive illumination than is the case in less productive waters. It is also possible that light inhibition of phytoplankton is to some extent an artifact, since during exposure of bottles, the algae are exposed to inhibiting radiation longer than is the case in nature, where they can move vertically. It has been found that in bottles which are moved vertically by ten meters each half hour, light inhibition of photosynthesis is weaker than in nonmoving bottles. Still, however, this effect apparently does occur under natural conditions: we know for instance, (Koblentz-Mishke, 1971) that the maximum ratio of chlorophylls *a:c* is present at the depth of the light optimum of photosynthesis.

The data mentioned earlier, from measurements *in situ*, were used to plot generalized light curves of the photosynthesis of phytoplankton living under various ecologic conditions--for various trophic zones of the tropical area. The curves are the envelopes of the fields of points on the graphs relating primary production to level of illumination at the depth of measurements (Fig. 6a) and standardized curves for the maximum of photosynthesis (Fig. 6b). The optimal irradiation in the tropical area is usually between 30 and 100 cal/cm^2•day, averaging 70 cal/cm^2•day, which amounts to 15-50% of the mean incident PhAR. Quite different curves are produced for highly eutrophic inshore zones: here the maximum photosynthesis is observed at the surface of the sea at the highest values of underwater irradiation observed anywhere under these ecologic conditions.

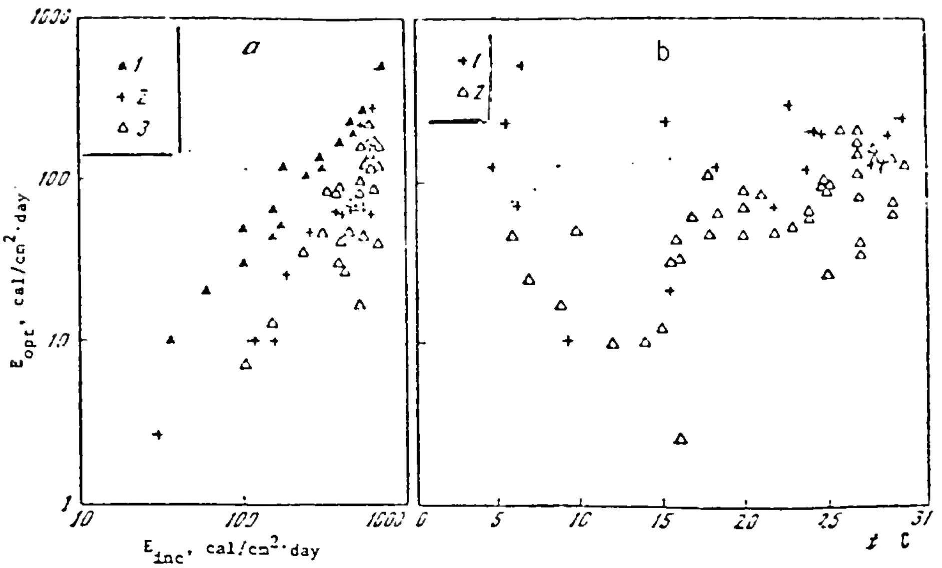


Fig. 5. Comparison of energy of irradiation optimal for AN (E_{opt}), with incident radiation (E_{inc}) (a) and temperature (t,°C) at optimum depth (b): a: 1, optimum AN at surface; 2, station with stratified water; 3, station with mixed water or without hydrologic data; b: 1, optimum AN at surface; 2, other stations.

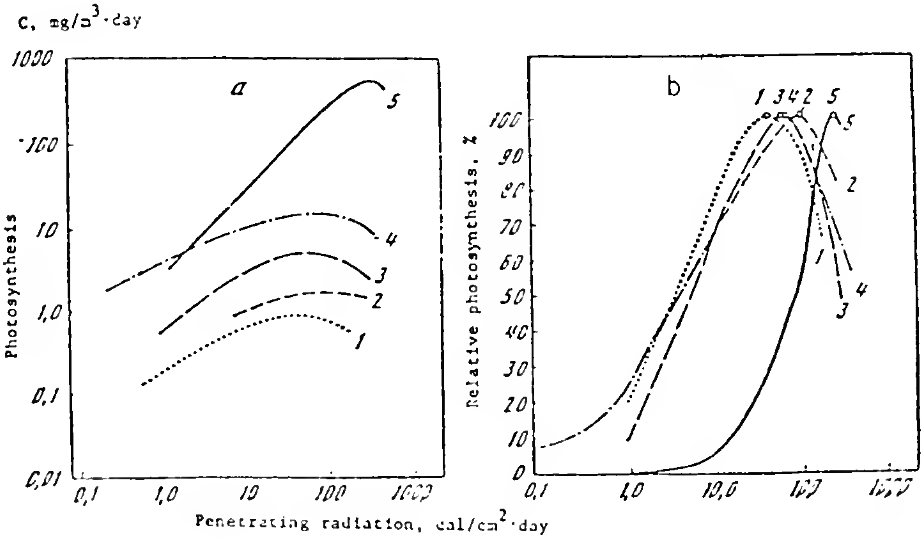


Fig. 6. Light curves of photosynthesis of phytoplankton in the tropical area: a--photosynthesis, mg C/m^3·day; b--same, % of maximum. Abscissa shows penetrating radiation, cal/cm^2·day. Primary production at surface, mg C/m^3·day: 1, < 2; 2, 2-5; 3, 5-10; 4, 10-100; 5, > 100.

As we study the light factor, it is quite important to determine the effectiveness of the utilization of light energy in the process of photosynthesis. We know that as one mole of CO_2 is fixed into the products of photosynthesis, 112 kcal of light energy is absorbed, or 9.36 cal/mg C. Expressing the data from measurements of photosynthesis in energy units and relating them to the quantity of energy available to plants, we can determine the energetic effectiveness of this process. The phytocenosis tends toward the upper, naturally, unattainable limit of this effectiveness during the course of its evolution. The maximum energy yield of photosynthesis under conditions of scattered long-wave radiation is not over 27%, while for white light the limit is considered to be 20%. The maximum quantum effectiveness is estimated as 8-12% (Rabinovich, 1959). In hydrobiology, the concept of energy effectiveness of photosynthesis has not yet been established. Of 6 formulas for the calculation of effectiveness (Patten, 1961d), only one, in the opinion of Platt (1969) satisfies the basic requirement of nondimensionality:

$$Q = E_0^{-1} \int_0^{=} P_z dz,$$

where P_z is the photosynthesis at depth z, expressed in cal/m^3, $E_{\bar{0}}$ is the light energy striking the surface of the sea (cal/m^2).

This integral effectiveness has been repeatedly estimated by various authors for various points in the World Ocean (Vinberg, 1960; Ryther, 1962). According to calculations for waters with various gradations of primary production, approximately 0.01 to 5% of the incident light energy is actually utilized in the process of photosynthesis; the energy effectiveness of photosynthesis of phytoplankton increases with increasing productivity of a region.

The true effectiveness of photosynthesis in individual samples taken from various depths VQ_z^t can be estimated for a layer 1 m thick by the use of an equation similar to that used in plant physiology:

$$Q_z^t = \frac{P_z}{\int_{400}^{700} \varkappa_p(\lambda) E_z(\lambda) d\lambda},$$

where E_z is the penetrating radiation at depth z, cal/m^2; $\varkappa_{\bar{\bar{p}}}$ is the index of absorption of light energy by phytoplankton pigments, λ is wave length. We (Koblentz-Mishke et al., 1975) have estimated the energy effectiveness Q_z^t in the equatorial and Peruvian upwellings of the Eastern Pacific Ocean. In these areas, Q_z^t increased from 2% at the surface to 20% at the depth reached by 1% of the light (Fig. 7).

To calculate Q_z^t, we must obtain absorption spectra of the phytoplankton pigments and detailed spectral characteristics of the penetrating radiation. These measurements have only recently become

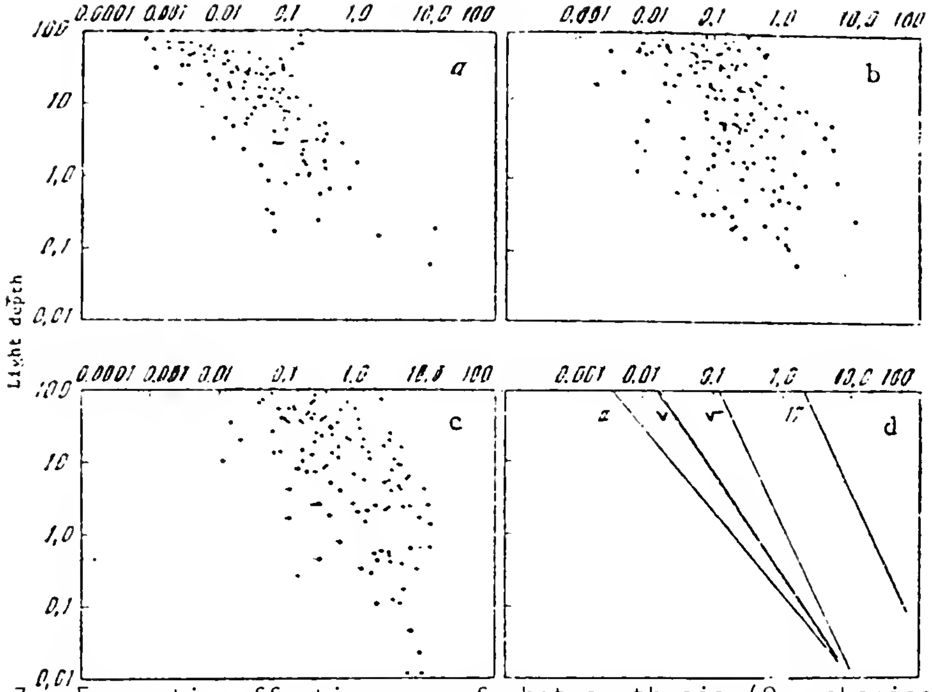


Fig. 7. Energetic effectiveness of photosynthesis (Q_z, abscissa) in regions with varying levels of primary production at the surface (mg C/m^3·day): a, < 2; b, 2-10; c, > 10; d, regression lines for graphs a, b, and c and for data on Q_z^t obtained during the 17th voyage of the research vessel AKADEMIK KURCHATOV (17). Ordinate shows light depth (% of penetrating radiation).

possible, with the appearance of immersible monochromators (Morel, 1973; Smith, 1973; Pelevin, Kel'balikhanov, 1974). Since previous optical measurements are not suitable for calculation of Q_z^t, we have calculated coefficient Q_z, i.e., the ratio of photosynthesis to total attenuation of light by pigments, water and impurities (α), using the following equation:

$$Q_z = \frac{P_z}{E_z(1-10^{-\alpha})} .$$

This coefficient Q_z was calculated for the 77 stations we have mentioned (Fig. 7); its maximum value was found at the lower boundary of the zone of photosynthesis. The effectiveness of photosynthesis here averages 10%, at some stations--20%, near its limiting value. Closer to the surface, Q_z decreases in oligotrophic waters more strongly than in mesotrophic and eutrophic ones. The main reason for this difference is that in the oligotrophic regions, the water absorbs a greater fraction of the light energy than at the same optical depths in richer regions. According to our results, in a mesotrophic region, the attenuation of penetrating radiation by pigments at the surface is 1%, increasing to 5% of the total attenuation at the depth reached by 1% of the light, while in a eutrophic region, the corresponding values are 50% and 80%. Thus, the difference between eutrophic and mesotrophic regions at the surface is a factor of 50, and at the 1% light-penetration depth--a factor of 16 (Koblentz-Mishke et al., 1975). This is almost proportional to the mean difference of Q_z in Fig. 7, d: 5.5 times at the surface, 2 times at the depth of 1% light penetration. These simple calculations confirm the fact that the light energy absorbed by phytoplankton pigments in mesotrophic waters is used in photosynthesis with effectiveness equal to that of eutophic waters.

The values of energetic effectiveness of photosynthesis obtained indicate that, at least in the lower portion of the euphotic layer, the radiocarbon method of measurement of primary production yields quite realistic results. At greater depths, clearly overestimated data are obtained, apparently a result of methodologic measurement errors.

The possibility of estimating the influence of environmental factors on photosynthesis by means of energetic effectiveness is also quite important.

Conditions of mineral nutrition. The study of the variation of primary production of the oceans with conditions of mineral nutrition is a significantly more difficult task than the study of its variation with the influence of light, due to the interconnection and interaction of the elements of mineral nutrition, due to the fact that in oceanographic practice their secondary characteristics are determined, and especially due to the existence in certain cases of feedback between the production and concentration of nutrients.

The demand of phytoplankton for various nutrient elements has been studied to widely varying extents. Phosphorus has been comparatively well studied, silicon to a lesser extent, nitrogen still less, particularly in the ammonia form, and almost no studies of iron demand have been made. As concerns the role of microelements and biologically active substances, the literature contains only a few more or less probable hypotheses. The primary source of nutrient substances is the reserve of the substances, which is accumulated in deeper waters as a result of the decomposition of organisms, then rises into the photosynthetic layer. A second source of supply of nutrient elements for algae is their regeneration in the photosynthetic layer itself in the process of decomposition of organic compounds by bacteria (Dugdale, Goering, 1967) and by zooplankton. The rate of regeneration of various nutrients is not identical, and, in general, depends on the temperature and relationship between the quantities of phytoplankton and zooplankton. In the tropics, it occurs more rapidly than in the temperate regions, due to the high temperature and as a result of the higher relative quantity of zooplankton. A third source is the arrival of nutrients with river runoff from the land (Sutcliffe, 1972) and upon mineralization of organic matter in shelf sediment. This source is important only in the seas and in the inshore areas of the ocean. One important source of nitrogen is the atmosphere. Nitrogen enters the sea with rain in the form of ammonia and nitrates (Vaccaro, 1965), and is also fixed by blue-green algae (Carpenter, 1973; Mague et al., 1974).

It is generally acknowledged (Ketchum et al., 1958) that nitrogen and phosphorus rise into the layer of photosynthesis in the same ratio (N:P = 15) that they are found in the phytoplankton. In the photic layer, due to the different rates of regeneration and loss of these elements, their ratio varies--nitrogen becomes relatively scarcer than in the deeper water. The lower the significance of the upward flow in the supply of alagae with elements of mineral nutrition in comparison to regeneration of these elements in the photosynthetic layer, the stronger the depression of the N:P ratio. Therefore, this ratio is a good index of the degree of limitation of primary production by conditions of mineral nutrition (Ketchum et al., 1958; Maksimova, 1973).

Vedernikov (1976a) compared the concentration of nitrates and phosphates in most regions of the World Ocean (Fig. 8). The N:P ratio was almost never normal (although if ammonia nitrogen is included in the analysis, such cases might be more frequent). Furthermore, when the concentration of nitrates decreased to less than 1 μg·atom P/ℓ, the content of phosphates remains at the same level (approximately 0.1-0.2 μg·atom P/ℓ). This level should not lead to extreme phosphorus "starvation" of marine planktonic algae, since the limiting concentrations of phosphates for the growth of cultures are usually < 0.15-0.55 μg·atom P/ℓ (Ketchum, 1939; Goldberg et al., 1951; Strickland, 1965; Thomas, Dodson, 1968). A concentration of nitrates of < 1 μg·atom N/ℓ , however, should cause significant nitrogen "starvation of marine planktonic algae (see Fig. 9).

Analyzing the data on the concentration of dissolved phosphates and nitrates, we can conclude that nitrogen plays a primary role as the limiting factor of the existence of marine planktonic algae. Enrichment experiments performed in various regions have shown that the limiting elements are most frequently nitrogen, phosphorus and iron, and in certain cases, silicon and trace elements (Co, Mn, Mo, Zn, Cu).

However, these experiments have shown that the influence of nutrients is different in short-term and in long-term experiments. Several hypotheses have been proposed to explain this, but the data presently available indicate only that long-term enrichment experiments are more reliable than short-term experiments in determining the elements which limit production. We can conclude that in most regions of the World Ocean, nitrogen and, less frequently phosphorus, regulate the level of primary production. Exceptions are regions of intensive upwelling, where the main factor limiting production may be the shortage of forms of iron which can be utilized by the phytoplankton and of trace elements. In 2-5-day experiments performed in the "juvenile" waters of upwellings, the addition of iron and trace elements, chelates or their mixtures led to a significant increase in production (Barber, Ryther, 1969; Barber et al., 1971). Barber et al., assume that natural organic chelators, liberated by the organisms as the surface water "ages," might be partially responsible for the increase in the growth rate of phytoplankton to the north and south of the equator in the eastern Pacific.

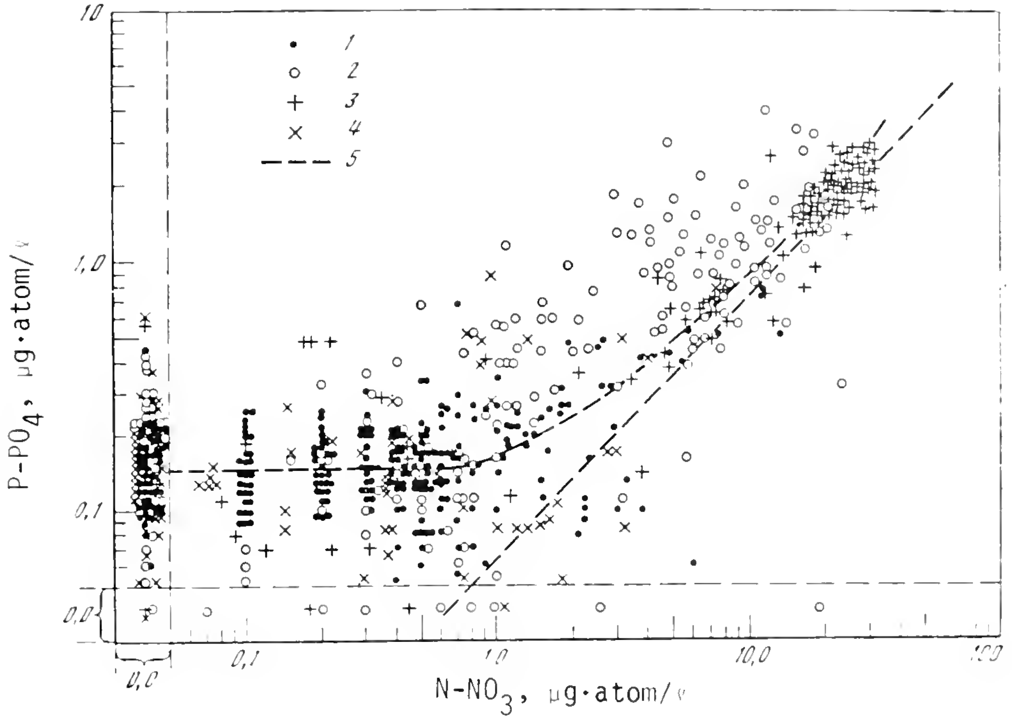


Fig. 8. Relationship between logarithm of concentration of nitrates and phosphates in the surface layer of various regions of the World Ocean. 1, Indian Ocean; 2, Pacific; 3, Atlantic; 4, Barents Sea; 5, line representing N:P = 15.

Some hold the opinion that it is hard to find a better "fertilizer" than the deep water which rises in the regions of upwelling. However, the favorable effect of deep water on the photosynthesis of phytoplankton is not immediately felt, due to the depressing influence of nonchelated heavy metals, which disappears when this water is held in darkness.

Enrichment experiments conducted in the southwest Atlantic and in the Caribbean have shown that the degree of influence of nutrients on the level of primary production in waters of low productivity in the low latitudes is several times greater than in highly productive waters in the higher latitudes (Kabanova, 1972; Kabanova et al., 1974a,b).

Comparison of level of primary production and conditions of mineral nutrition. At the present time, it can be considered firmly established that in most regions of the World Ocean, primary production is limited by a shortage of the elements of mineral nutrition. On the global scale, the concentration of nutrients and the level of primary production change over the water area in a similar manner.

For individual regions of the ocean, the correlation coefficient between production and the concentration of nutrients has been calculated. For example, in the northern part of the Indian Ocean, a positive relationship has been found between the mean zonal values of primary production and the content of phosphates, nitrate nitrogen and silica in the upper 100-meter layer; the correlation coefficients are +0.68; +0.83 and +0.88 (Maksimova, 1972). In the more productive waters of the near-antarctic region of the southwestern Atlantic, the correlation coefficients between phytoplankton production in the surface layer and the content of phosphates and nitrates is much lower: +0.42 and +0.44 (Kabanova et al., 1974a,b).

In regions of low productivity, where the concentration of nutrients approaches analytic zero, the variation of production with the content of these elements is difficult to trace due to the significant measurement errors.

Extensive materials collected in the tropical Pacific, Indian and Atlantic Oceans were used (Fig. 9a) to compare the concentration of nitrates and primary production at the surface (> 1300 stations) and at the depth of maximum AN, i.e., in the layer of optimal illumination (200 stations) (Fig. 9b). The relationship between the values of primary production and concentration of NO_3 is described in log-log coordinates by an S-shaped curve. Since at low concentrations of nitrogen, its reduced forms play a significant role in the mineral nutrition of algae (Thomas, 1970), determination of the concentration of NO_2 and NH_4 would result in some straightening of the initial slope of the curve, and it might be described by the Michaelis-Menten equation. The relationship between the concentrations of nitrate nitrogen and photosynthesis at the level of optimal illumination is described by practically the same curve as for the surface.

The effect of nutrients on production can be represented in two ways. In the opinion of some authors (Fedorov, 1970; Koblentz-Mishke et al., 1975), under favorable conditions of mineral nutrition, as a result of structural changes in the phytoplankton community, a denser population of phytoplankton exists than in the poorer regions, more completely absorbing solar energy and using it for more intensive summary photosynthesis. Other authors (Baslavskaya, 1961; McAllister et al., 1964; Thomas, Dodson, 1972; Kabanova et al., 1974a,b) believe that an improvement in the conditions of mineral nutrition influences primarily the effectiveness of the action of the photosynthetic apparatus of each individual cell.

The reality of the first mechanism is beyond doubt. This is indicated by the positive relationship between the concentration of nutrients and the abundance of phytoplankton (Semina, Tarkhova, 1970) and the concentration of chlorophyll (Taniguchi, 1972; our data--Fig. 9c).

The second mechanism has been confirmed by data on the AN under various conditions of mineral nutrition.

Poor mineral nutrition conditions for phytoplankton may result in a decrease in the AN: this is shown in enrichment experiments with natural populations and cultures of planktonic algae. For natural populations of phytoplankton, inhabiting waters with a high content of

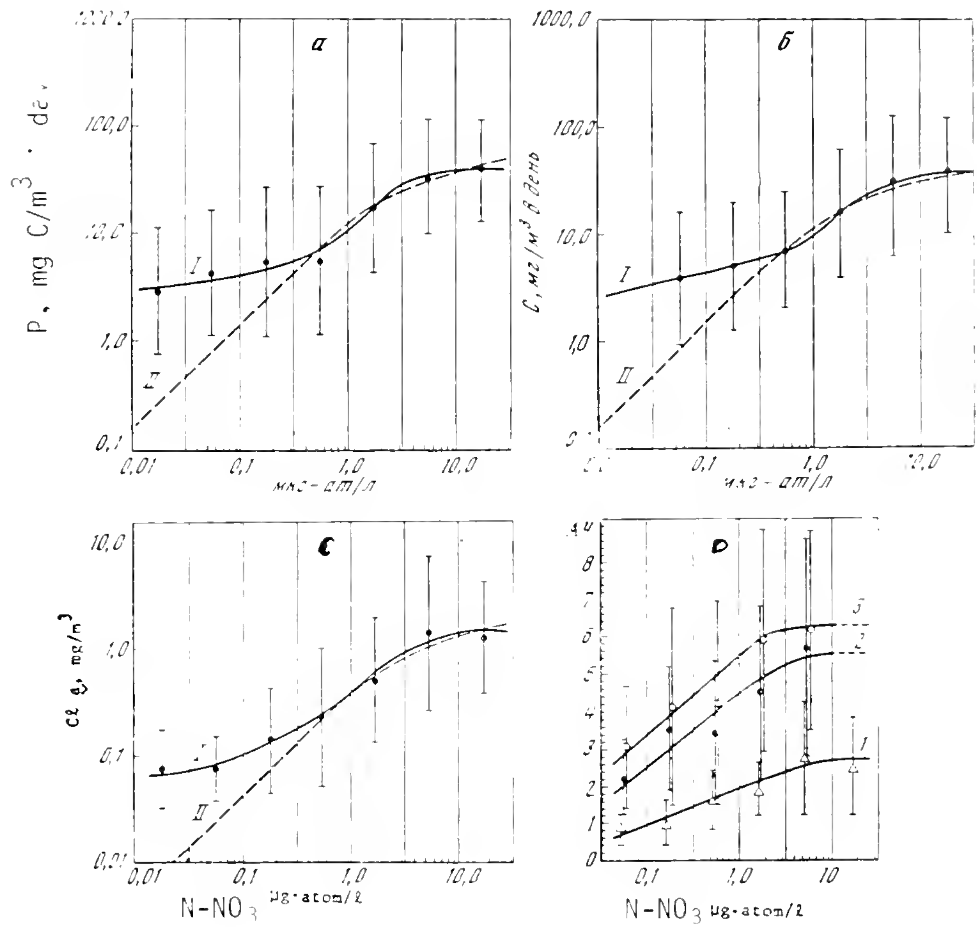


Fig. 9. Relationship of nitrates with production at the surface (a), production in the layer of maximum AN (b), content of chlorophyll a in the layer of maximum AN (c), and hourly AN (d): a, b, c, tropics; d, World Ocean; 1, t° = 0-10°C; 2, t° = 10-20°C; 3, t° = 20-30°C; I, regression lines; II, Michaelis-Menten curves. Vertical line sections show mean square deviations.

nutrient salts, higher values of AN are characteristic (Saijo, Ichimura, 1960; Aruga, Monsi, 1962; Ichimura, Aruga, 1964; Thomas, 1970; Malone, 1971).

A positive connection has also been established between AN and the conditions of mineral nutrition in the seasonal aspect (Vedernikov, Solov'yeva, 1972).

To analyze the variation in values of AN, measured at the optimal or neaar-optimal level of illumination (AN_{opt}) with the content of nitrates, 370 parallel determinations of chlorophyll a, production and nitrates in various seas and oceans were analyzed. Only the results of measurement of AN in samples containing 0.1-10 mg/m^3 of chlorophyll a were used, since with lower contents of chlorophyll the random error of determination of AN increases rapidly (Vedernikov, 1973), while with higher contents, the high population density may have a negative influence on photosynthetic activity of the phytoplankton.

It was found (Fig. 9d) that for all temperature intervals, there is a positive connection between the content of nitrates and the values of AN. As the nitrates increased from the level of analytic zero to 3-5μ g·atom/ℓ, the mean value of AN increased by a factor of 2-3. This increase was statistically reliable.

Rather high values of AN with practically zero content of nitrate nitrogen resulted, apparently, from the presence of ammonia nitrogen in the water. It is possible that this form of nitrogen and certain dissolved organic substances containing the amino group act as a buffer, preventing the extreme degree of nitrogen starvation of phytoplankton when the nitrates in the water are completely exhausted (Thomas, 1970).

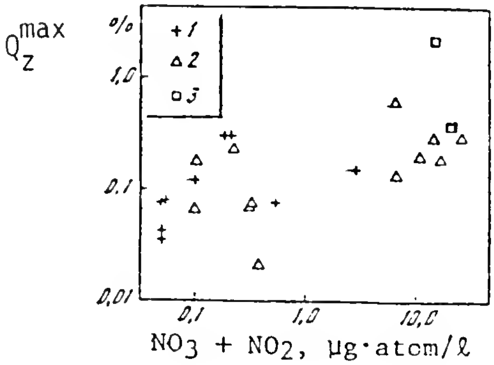


Fig. 10. Maximum energy effectiveness of photosynthesis (Q_z^{max}, %) and concentration of oxidized forms of nitrogen (μg·atom/ℓ) for each station. Stations with primary production of: 1, < 2; 2, 2-10; 3, > 10 mg C/m^3·day.

The relationship between AN_{opt} and phosphates is weaker than the relationship with nitrates (Vedernikov, 1976). This confirms once more that nitrogen limits primary production more strongly than does phosphorus.

Data on the variation of AN_{opt} with the conditions of mineral nutrition agree with the assumption that mineral nutrition not only regulates the structure of the photocenosis, but also determines the level of functioning of the individual photosynthesizing units. The same conclusion results from station-by-station comparison of the maximum values of effectiveness of photosynthesis with the concentration of oxidized nitrogen at the same depths--at the bottom of the photic layer: the effectiveness of photosynthesis upon threshold illumination is positively related to the concentration of nitrates and nitrites (Fig. 10).

Thus, the conditions of mineral nutrition of phytoplankton influence production, acting not only on the structure of a community, but also on the intensity of functioning of the individual organisms.

Temperature. The study of the influence of temperature on the production characteristics under natural conditions is greatly hindered by the fact that temperature in nature is positively correlated with illumination and negatively correlated with the concentration of nutrient salts and, therefore, influences photosynthesis not only directly but also indirectly. Also, in determining production by the radiocarbon method, the effect of temperature may depend not only on the intensity of photosynthesis, but also on the relationship between photosynthesis and respiration, since these two processes cannot be distinguished by the ^{14}C method. The close interrelationship of the temperature factor to light and the effect of nutrients has resulted in the fact that most authors analyze this factor in combination with the others.

It has been established that the light adaptation of algae is closely related to the temperature conditions. Experiments carried out under semilaboratory conditions have shown that "dark" phytoplankton, living in the lower portion of the euphotic zone, is adapted to lower temperatures than "light" phytoplankton. Furthermore, it is thought that adaptation to low levels of illumination is an apparent phenomenon, while in actuality the corresponding light curves of photosynthesis are natural for algae living at low temperatures.

Experiments with both cultures and natural populations have shown that algae appertaining to various systematic groups differ as to temperature options of photosynthesis and rates of cell division. A low temperature optimum is observed in diatoms, a higher optimum in green algae (Eppley, 1972). The higher the temperature optimum of the algae, the more intensive its photosynthesis and the higher the rate of division of which it is capable. The position of the temperature optimum of photosynthesis and the growth of algae are influenced much more by temperature conditions of growth and habitat temperature than by taxonomic composition (Barker, 1935; Braarud, 1961; Ichimura, Aruga, 1964, 1965). Below the temperature optimum, there is a relationship between the rate of assimilation of CO_2 and the temperature which is near exponential (Heath, 1972). In cultures of various planktonic algae grown at 20°C, the ordinary values of temperature coefficient $Q_{10} = 2\text{-}3$ are characteristic for broader temperature ranges (20° or 30°C). However, for narrower temperature ranges (5-10°C), the values of Q_{10} are more varied, for example for green algae from 1.3 to 4.8, higher at low temperatures than at high temperatures (Rabinovich, 1959, page 39). This apparently results from the fact that in the area of low temperatures they control the dark reactions which are the main factor limiting the rate of the entire process of photosynthesis (Heath, 1972, page 201). At higher temperatures, dark reactions occur more rapidly, Q_{10} decreases, the light energy absorbed by the chloroplasts is not sufficient for assimilation of additional quantities of CO_2, and photosynthesis begins to be limited by light, even when its intensity is quite high.

The influence of the temperature factor on the photosynthetic activity of natural populations of phytoplankton has been less studied. The values of Q_{10} for the phytoplankton of Japanese lakes and the Oyashio Current in 10-20°C temperature interval is equal to 2.0 (Ichimura, Aruga, 1959; Ichimura et al., 1962). It was found without preliminary adaptation of the algae. After such adaptation, the temperature coefficient in cultures of certain algae may decrease significantly--sometimes by a factor of 2 (Steemann Nielsen, Jorgensen, 1968). These authors believe that the reason for this is the great increase in the quantity of photosynthetic enzymes (per unit of active pigment and per cell) at low temperatures.

Finenko and Lanskaya (1971), using cultures of the same species, taken from different latitude zones, showed that algae adapted to low temperatures decreased the rate of cell division significantly more slowly as the temperature drops than do the same algae which have vegetated at higher temperatures.

A comparison of temperature and primary production under optimal light conditions was conducted on the basis of the data from almost 200 stations _in situ_ in the tropics of the Pacific and Atlantic Oceans (Fig. 11a). There is a general tendency toward feedback between the level of primary production and temperature. This tendency results from the fact that the temperature is negatively correlated with the concentration of nutrients: a decrease in the temperature of the euphotic layer is observed in areas where the deep waters rise. In zones of different content of nitrates, the temperature has no influence on production ($N\text{-}NO_3 < 1.0$ μg•atom/ℓ). Apparently, the temperature, in and of itself, has no influence on the level of production in the tropics.

However, analysis of the data of 360 stations _in situ_ in various latitude areas has shown that the temperature has a _positive_ effect on AN. An analysis was conducted of the relationship of temperature with AN for marine phytoplankton inhabiting waters with poor conditions ($N\text{-}NO_3 < 0.1$ μg•atom/ℓ), moderate conditions ($N\text{-}NO_3 = 0.1\text{-}1$ μg•atom/ℓ) and good conditions of mineral nutrition ($N\text{-}NO_3 > 1.0$ μg•atom/ℓ) (Fig. 11b).

In all three zones, there is a positive correlation between the values of AN and temperature. As the temperature rises from 5° to 25°C, the values of AN increase, with a low content of nitrates, by a factor of 3.9; with a moderate content of nitrates, the increase is by a factor of 2.9, and when the nitrate content is high, the increase factor is 2.2; this increase is reliable with a high level of significance. The curves show that the temperature influences the assimilation activity of the chlorophyll practically only up to 20°C. The range of 20-30°C can be considered optimal for the values of AN. At 20-25°C, they are 1.03-1.13 times higher than at 25-30°C, but the difference between the mean values of AN at these two levels is not reliable, which is probably explained by the adaptation of the algae to high temperatures. A temperature of the surface waters of over 25°C is observed in the tropics, and in summer in the inshore waters of the temperate latitudes. Adaptation to this high temperature is apparently possible

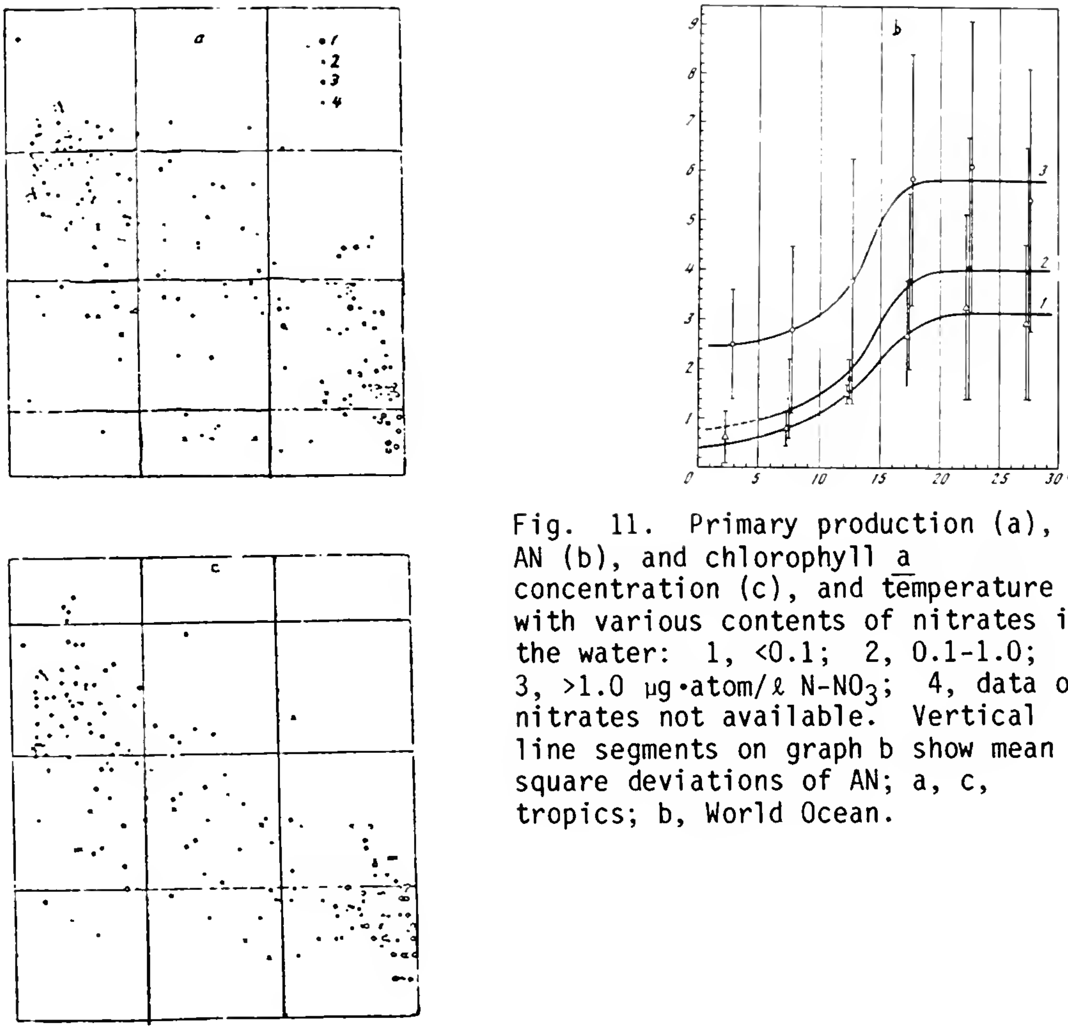


Fig. 11. Primary production (a), AN (b), and chlorophyll a concentration (c), and temperature with various contents of nitrates in the water: 1, <0.1; 2, 0.1-1.0; 3, >1.0 µg·atom/ℓ N-NO_3; 4, data on nitrates not available. Vertical line segments on graph b show mean square deviations of AN; a, c, tropics; b, World Ocean.

in both cases. Thomas (1966) showed that the optimal temperature for the growth rate of the tropical algae Chaetoceros and Nannochloris lies in the 27-37°C interval. Williams and Murdoch (1966) found no depression of assimilation activity of chlorophyll in the summer months at temperatures of 25-30°C.

The curves presented in Fig. 11b were used to determine the values of Q_{10} for various temperature intervals (Table 2).

The mean value of Q_{10} for zones with different contents of nitrates was found to be 2.2 in the 0-20°C interval, 1.7 in the 0-30°C interval. The former of these values coincided with the value of Q_{10}, obtained for the littoral waters long the Atlantic coast of the USA (Williams, Murdoch, 1966). From this it follows that for the mean assimilation activity of chlorophyll under natural conditions over a broad temperature interval, the most probable values of Q_{10} are close to 2, at least in mesotrophic and eutrophic waters. The values of Q_{10} for individual 5°C intervals were maximal at 10-15°C, decreasing rapidly with an increase in temperature, less rapidly with a decrease in temperature. The decrease in Q_{10} with increasing temperature is a common phenomenon in "sharp" experiments. The slow decrease in AN with a decrease in temperature apparently results from an adaptive increase in the content of photosynthetic enzymes in the cells.

Table 2. Values of Q_{10} for various temperature intervals in waters with low, medium and high content of nitrates.

Temperature Interval, °C	Content of $N\text{-}NO_3$, μg·atom/ℓ		
	<0.1	0.1-1.0	>1.0
0- 5	2.2	1.6	1.1
5-10	3.4	2.3	1.5
10-15	3.8	3.9	2.6
15.20	2.1	1.8	1.4
20-25	1.0	1.0	1.0
25-30	1.0	1.0	1.0
0-20	2.7	2.2	1.6
0-30	2.0	1.7	1.4

The decrease in the value of Q_{10} with improvement of the conditions of mineral nutrition is notable. It results, first of all, from the more rapid increase in AN with improvement of the conditions of mineral nutrition in warm waters in comparison with colder waters and, secondly, from the higher limiting concentrations of nitrates in these waters (see Fig. 9d). An analogous relationship between the values of Q_{10} and the conditions of mineral nutrition can be obtained upon analysis of the curves of the variation in the P/B ratio with phosphate content at various temperatures (Riley et al., 1949). According to our calculations, Q_{10} for the 5-25°C interval is 2.7 with a low content of phosphates in the water (0.1 μg·atom/ℓ), and 1.6 with a high phosphate content (0.5 μg·atom/ℓ). These figures are close to those obtained by us for the 0-20°C interval.

The contradiction between data on the influence of temperature on photosynthesis and AN becomes clear when we compare the temperature and concentration of chlorophyll in the tropical portion of the Pacific, Indian, and Atlantic Oceans (Fig. 11c). Whereas in the waters with a concentration of NO_3 <1.0 μg·atom/ℓ, the content of chlorophyll decreases slightly with an increase in temperature, in waters with a good supply of nitrogen (>1 μg·atomℓ), it is inversely proportional to temperature. We find that in regions of the ocean with poor and moderate conditions of mineral nutrition (NO_3 <1.0 μg·atom/ℓ), the slight increase in AN with temperature is compensated for by a decrease in the concentration of chlorophyll, as a result of which production is independent of temperature; in eutrophic regions ($N\text{-}NO_3 > 1.0$ µg·atom/ℓ), AN increases very slightly with temperature, while the concentration of chlorophyll decreases rapidly; as a result, a drop is observed in the level of photosynthesis. In this last case, the temperature does not influence the rate of photosynthesis directly, but rather as a factor which is negatively correlated to the concentration of nutrient salts.

Comparison of results obtained under laboratory and natural conditions. In discussing the influence of light on the photosynthesis of phytoplankton, we should make one general comment concerning the impossibility of reproducing all of the parameters of the light field *in situ* under laboratory conditions. This is particularly true of the top water layer of high irradiation. With "inhibiting" irradiation, suppression of photosynthesis is usually (but far from always) observed. With the same irradiation under laboratory or deck-incubator conditions, the light curves of photosynthesis reach a plateau instead of descending. We can name four probable causes for the decrease in photosynthesis beneath the surface of the sea: inactivation of chlorophyll by excess energy; inhibition of the process by the UV component of the light field, not considered in measurements of PhAR; incomplete utilization of the light flux, which is insufficiently polarized at the surface; and underutilization of light fluctuating as a result of the focusing effect of the irregular surface of the sea. The lack of inhibition of photosynthesis in highly eutrophic water speaks in favor of UV radiation as the cause of the drop in photosynthesis near the surface, since these waters contain a yellow substance which absorbs short-wave radiation.

Thus, the rapid displacement of the position of the light optimum described above can be explained not only by adaptation of the phytoplankton, but also by the fact that the energy is underutilized in the near-surface layers due to certain special properties of the light field or a combination of this field and the peculiarities of the pigment system. Illumination conditions may be considered "optimal" at the depth where this underutilization stops. If this depth changes only slightly at a given point in the ocean, different quantities of light energy will reach the point as the weather changes, leading to a shift of the optimum on the light curves of photosynthesis. The position of the "light optimum" of photosynthesis in this case is determined not by the physiologic peculiarities of the phytoplankton, but rather, by the parameters of the light field, which explains the slight variation in the position of the "light optimums" of photosynthesis as a function of temperature, in comparison to the incident radiation (Fig. 5).

The absolute values of the "light optimums" for photosynthesis, obtained under natural conditions and in cultures, are basically similar, exceptions being the data observed in cloudy weather, when the light optimum of photosynthesis was found to be at much lower irradiation than is usually observed under laboratory conditions. The threshold value of irradiation under natural conditions was found to be related not to the systematic composition of the phytoplankton (as was indicated in cultures), but rather with the ecologic conditions. If we consider that at the threshold value of irradiation, the light curves of effectiveness of utilization of sunlight in photosynthesis bend, we find that its threshold intensity in oligotrophic and mesotrophic regions is observed at the depth to which ≤1% of the subsurface radiation penetrates, in eutrophic waters--about 10%.

Data on the absolute effectiveness of utilization of solar energy can be used to evaluate the radiocarbon method of measurement of primary production. The maximum value of this effectiveness is about 20%. This is the effectiveness which is observed at the bottom of the euphotic layer. This means that the radiocarbon method, at least in the lower portion of the layer of photosynthesis, provides quite realistic results.

A significant portion of the disagreement obtained in the study of light as a factor in photosynthesis under laboratory and natural conditions depends on the difference in the spectral composition of the light. Due to chromatic adaptation, phytoplankton from the lower portion of the photosynthetic layer has a set of pigments adapted to the specific spectral composition of the penetrating radiation. This phytoplankton, when placed in incubators with neutral-density light filters, absorbs a much lower fraction of the radiant energy than in the sea at the depth at which it lives. As a result, the threshold of photosynthesis in incubators is observed at higher levels of irradiation than _in situ_. The situation is somewhat improved when blue light filters are used, but even in this case, the imitation of the spectral composition of the penetrating radiation is imperfect, particularly in highly productive inshore waters.

Table 3. K_s (μg·atom N/ℓ) for the rate of uptake of NO_3 in cultures and for the relationship of concentration of oxidized forms of nitrogen to primary production, concentration of chlorophyll and AN.

Objects studied	K_s	Reference
Cultures	Rate of uptake	Eppley et al., 1969
Small oceanic diatoms and coccolithophorids	0.1- 0.7	
Neritic diatoms	0.4- 5.1	
Neritic dinoflagellates	3.8-10.3	
Small flagellates	0.1- 0.4	
Natural populations of the tropics of the Pacific, Indian and Atlantic Oceans	Relationship of nitrates to primary production At surface 3.33 At optimum AN level 2.56 Relationship of nitrates to chlorophyll at optimum AN level 4.2	Our data
Tropic and temperate zones of the ocean, 20-30°C	Relationship of nitrates to optimal AN 0.17	Vedernikov, 1976b

Natural conditions of mineral nutrition are created in laboratories much more easily than natural light field conditions. The only exceptions are the peculiarities of nutrition which depend on light. For example, the rate of absorption of nutients differs under natural conditions and in incubators. In general terms, there is great similarity between the specifics of mineral nutition under laboratory and natural conditions. This is true primarily of nitrogen.

Under laboratory conditions, the relationship of the concentration of nutrients to the rate of their uptake and growth rate is described by hyperbolic curves, following the Michaelis-Menten equation. The constant of this equation represented by the symbol K_s is numerically equal to the concentration of nutrient substances at which the rate of their uptake or of growth of the algae reaches half of its maximum value. The value of K_s for these two processes in cultures of marine diatoms differs slightly. Under natural conditions in the tropics, the relationship between the concentration of chlorophyll is described by S-shaped curves, the right parts of which follow the Michaelis-Menten equation, while the left part is higher, due to underevaluation of ammonia nitrogen (Fig. 9). We can use the right portion of the curve to calculate K_s (Table 3). Comparing the values of K_s for cultures and natural populations, we see that the results produced for AN of natural populations and the absorption of NO_3 by small algae agree well. This is understandable, since in both cases the population density is considered in the calculation: K_s in this case represents the rate of processes in each individual cell or pigment unit. K_s for primary production and concentration of chlorophyll reflects the integral effect of the conditions of nitrogen nutrition on the entire phytocenosis. They have the greatest influence on the concentration of chlorophyll, while influencing the level of production somewhat less.

These data throw additional light on the problem we have already discussed, the mechanism of action of the conditions of mineral nutrition on primary production. The results of determination of the effectiveness of utilization of solar energy in photosynthesis in mesotrophic and eutrophic waters have led to the hypothesis that the primary effect of the conditions of mineral nutrition occurs at the biocenologic level. Analysis of the relationship of AN with the conditions of nutrition, however, has indicated that the conditions of nutrition play a definitive role in the regulation of processes at the level of the organism as well. However, based on a comparison of K_s for AN and chlorophyll (see Table 3), we must conclude that this mechanism, except for regions with very low content of nutrients, is not of great significance for the development of populations of phytoplankton.

No clear relationship has been achieved under natural conditions between temperature and the production characteristics (except for AN). However, the results produced indicate that the effective temperature is manifested at the level of the organism, having no direct effect at the population level.

2. Production of Microflora. (Yu. I. Sorokin)

The microflora of the seas and oceans is represented by heterotrophic bacteria and fungi (mold, fungi, actinomycetes, yeast). Among these, the bacteria have the greatest significance from the standpoint of participation in production and metabolism of the community. Some researchers also include phytoplankton and heterotrophic zooflagellata among the marine microflora (Wood, 1965), but this is ecologically unjustified.

The microflora represent the most important components in the marine ecosystems (Sorokin, 1971a, 1971b, 1973c). It represents over 60%, usually about 80%, of the total energy flow passing through the heterotrophic portion of the community, and over 50% of all expenditures of the community in metabolism (Table 4, Fig. 12).

Considering that the effectiveness factor of biosynthesis (K_1) for bacteria is close to that of aquatic invertebrates--about 0.25--we must consider that the production of the microbial population is significantly greater than the total production of protozoa, and all remaining forms of zooplankton. Therefore, a reliable estimate of biomass, production and metabolism of the microbial population is a necessary condition for an accurate ecologic analysis of marine ecosystems. In this section, we shall study primarily the production phase, as well as a few problems of the biogeochemical activity of marine microflora, directly related to the processes of biosynthesis and destruction.

2.1 Methodologic Problems

In order to determine the productive significance of the microflora in marine communities, we must determine the characteristics of the vertical structure of microbial communities and their aggregation; biomass, production, and metabolic rate of the microbial population; sources of energy for bacterial biosynthesis; food value of microbes; contribution of microbes to production, metabolism and transformation of energy in marine ecosystems.

The production of microflora in bodies of water is determined by holding freshly taken samples of water in bottles for 12-24 h at the temperature *in situ*. The intensity of multiplication of the bacterioplankton in the bottles is measured on the basis of the increase in population (comparison of total number of bacteria at the beginning and at the end of exposure by direct counting) or by measurement of the intensity of biosynthesis. This is determined primarily by the radiocarbon method (Sorokin, 1971a, 1973g). The method was offered by Romanenko (1964) for fresh water. It is based on the existence of an empirical relationship between the dark assimilation of

Table 4. Elements in the balance equations of the basic components of the planktonic community in the equatorial Pacific Ocean, kcal/m^2·day (Sorokin, 1975a).

Component of Community	Ration	Production	Unassimilated Food	Expenditures for Metabolism		Coefficient K_i
Upwelling, 97° W						
Phytoplankton	---	33.0	---	---	---	---
Bacterioplankton	15.7	4.70	---	11.0	72%	0.30
Microzooplankton (Protozoa)	0.71	0.32	0.21	0.18	1%	0.45
Microzooplankton (Nauplii)	3.05	1.01	1.07	1.03	7%	0.33
Nonpredacious mesozooplankton	2.50	0.62	0.62	1.26	8%	0.25
Predacious mesozooplankton	3.30	0.82	0.66	1.82	12%	0.25
Zone of Divergence, 154° W						
Phytoplankton	---	6.30	---	---	---	---
Bacterioplankton	16.3	4.90	---	11.4	85%	---
Microzooplankton (Protozoa)	1.82	0.82	0.50	0.50	4%	0.50
Microzooplankton (Nauplii)	0.84	0.33	0.32	0.19	1%	0.32
Nonpredacious mesozooplankton	1.27	0.32	0.31	0.64	5%	0.31
Predacious mesozooplankton	1.13	0.28	0.22	0.63	5%	0.22

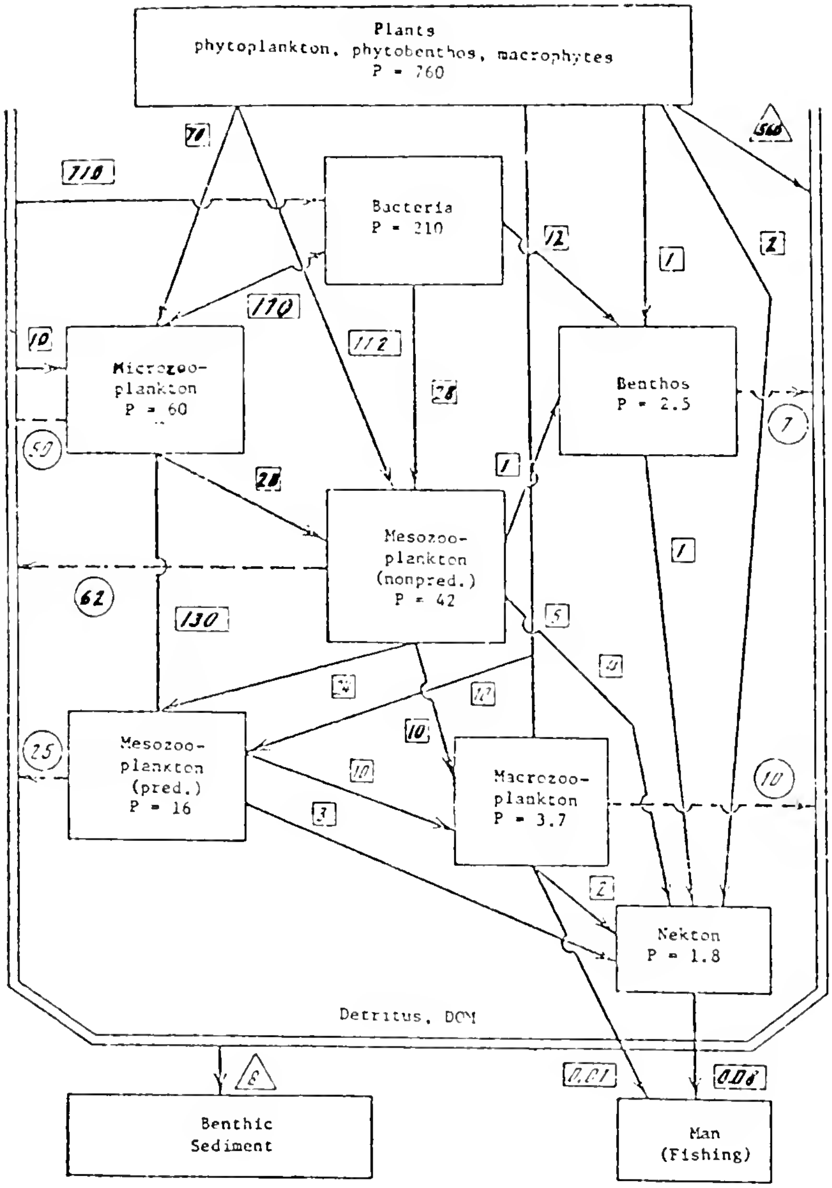


Fig. 12. Diagram of flows of energy (10^{15} kcal/yr) in the ecosystem of the World Ocean. P, production: figures in boxes--consumption by organisms of the next trophic level; figures in circles--nonassimilated food; figures in triangles--unconsumed production; DOM = dissolved organic matter.

CO_2 by heterotrophic bacteria and their production: in bacteria with different types of metabolism, it varies from 3% to 10%; for bacterioplankton in sea water it is approximately 5% (Sorokin, 1971a). Thus, the production of bacterioplankton P can be calculated by the equation P = 20 A (mg $C/m^3 \cdot day$), where A is the daily value of dark assimilation of CO_2, measured by the radiocarbon method (Sorokin, Kadota, 1972) in water from which the zooplankton and most of the phytoplankton has been removed by preliminary filtration through a screen of 7-10 μm mesh.

This method probably yields somewhat elevated values of production and respiration of the bacterioplankton (approximately 20-40% high) in water of the euphotic zone due to the elimination of consumers in the preliminary filtration, but not due to the so-called "bottle effect." This effect, described by ZoBell and Anderson (1936) results from the fact in that when water is stored for a long period of time in small bottles, intensive growth of heterotrophic bacteria begins. The intensity of multiplication is higher in small bottles, which is explained by the adsorption of organic matter onto the walls of the flasks, making the organic matter more accessible for the microflora. The observations of ZoBell long served as an argument against the use of the bottle method for the study of the intensity of bacterial processes in sea water (Steemann Nielsen, 1972; Banse, 1974); however, these arguments are based on a misunderstanding. The plate count method used in the experiments of ZoBell and Anderson considers only a small portion of the microbial population of the sea water (≤0.5%), which reacts more rapidly than the remainder of the microflora to the death of planktonic organisms in the samples. However, even for this small portion of the microbial population, the flask effect appears only after 2 or 3 days of exposure, whereas the standard exposure of bottled samples for determination of the production of bacteria and phytoplankton is not over 1 day. Many experiments have proven that there is no "bottle effect" in the multiplication of the entire microbial population in samples of natural water with exposures of up to 5 days at 20-25°C (Vinberg, Yarovitsyna, 1946; Czeczuga, 1960; Godlevska-Lipova, 1969; Romanenko, 1969).

There are methods of indirect estimation of bacterial production. One consists in determination of the time of generation of bacteria on the basis of the rate of washing of a microbial population out of a flowthrough cultivator (Jannasch, 1969). If we know the time of generation of bacteria and their biomass, we can calculate the production. Another method consists in the determination of the increase in microflora in an isolated sample on the basis of the change in the number of particles of a finely dispersed suspension, determined by means of a Coulter counter (Sheldon et al., 1973).

The degree of aggregation of marine microflora is determined by microscopy in a phase-contrast or luminescent microscope (Wood, 1965) or by the dimensional composition of particles in the suspension, established by means of a Coulter counter. The method of labeling of natural bacterioplankton in water samples by small doses of ^{14}C-labeled protein hydrolysate, with subsequent filtration on a filter with a pore diameter of 4-6 μm, which retains bacterial clumps, is also used (Sorokin, 1970b).

In order to establish the sources of energy for bacterial biosynthesis, we must comparatively evaluate the utilization of autochthonous and allochthonous organic matter by the microflora. In analyzing the energetics of a local ecosystem, it is important to obtain data on the degree of utilization of external dissolved organic matter, brought in by currents from other regions, since bacterial biomass thus produced (P_a) should be added to the primary production of the community (P_p) to calculate the total energy "input" of the ecosystem (Sorokin, 1971a, 1973c).

The nutrient value of marine microflora for aquatic animals is estimated by long-term cultivation of these animals, using a suspension of bacteria as food or by quantitative counting of microflora in the contents of various segments of the gut (Zhukova, 1954). However, the basic data on the nutrition of marine invertebrate microflora under conditions which are close to natural have been obtained in short-term experiments using bacteria labeled with ^{14}C or ^{32}P (Marshall, Orr, 1955; Sorokin, 1966, 1968). The use of ^{32}P can generate only qualitative data, since the labeled organic phosphorus in the bacteria is rapidly involved into the metabolism and is excreted from the organism of the consumer in the form of inorganic phosphate. The use of ^{14}C allows quantitative data to be generated, since ^{14}C is included into the carbon chains of the organic matter and is thus much more slowly excreted. The radiocarbon method can be used to determine the significance of bacteria in the spectrum of nutrition, to determine the magnitude of food rations, the assimilability of food by consumers, the rates of filtration and the dependence of intensity of nutrition upon the concentration of food (Sorokin, 1971a,b,c).

The results of measurement of biomass, production, and metabolism of a microbial community are expressed in calories under 1 m^2 per day. A coefficient of 0.92 is used to convert a unit of wet biomass of bacteria to calories, considering that the content of carbon in microbial biomass is 10% (Troitskiy, Sorokin, 1967).

2.2 Number, Biomass and Production of Planktonic Microflora in Communities with Various Levels of Productivity

In the overwhelming majority of works on marine microbiology, data were presented on the numbers of saprophytic bacteria growing in protein media, which gave not the slightest idea of the total microbial population. The available data, obtained by direct counting and by the use of ATP, show that the population and biomass of the microbes in the euphotic zone of unpolluted marine basins averages 1.5-2 times less than in fresh bodies of water with the same trophic level. This is apparently the result of the utilization by the microflora in the fresh waters of significant quantities of allochthonous organic matter arriving from the land.

Summary data on the mean population and biomass of planktonic microflora in various biotopes shows that in the euphotic zone of the eutrophic sea basins--estuaries, shallow bays, lagoons, and also in the highly productive zones of upwelling, where the primary production exceeds 1 g C/m^2 per day, the total population of bacteria is 1.5-5 million cl/ml, the biomass is 0.5-3 g/m^3 (Melberga, 1968; Karapetyan, 1971; Sorokin, 1971a,c, 1973a; Sorokin et al., 1975; Fedorov, Sorokin, 1975). Here, as in most marine biotopes, sporeless rod-type bacteria and micrococci predominate, measuring 0.3-1 x 1-2.5 μm. In eutrophic basins the mean volume of microbial cells is 2 to 4 times greater than in oligotrophic basins--averaging 0.8-1.5 μm^3.

The production of bacterioplankton in warm surface waters of eutrophic regions averages 0.2-2 g/m^3 per day (according to the data of the radiocarbon method). The duration of 1 generation (doubling time of the number of bacteria) is 15-40 h. The mean daily P/B coefficient is 0.5-1. The generation time and P/B coefficients of bacterioplankton as a whole depend less on the trophic level of the basin than on the temperature of the water (Sorokin, 1971a, 1973b, 1974; Karapetyan, 1971).

In the upper layer of the water of mesotrophic regions--waters in the temperate zone, the neritic zone of the tropical and subtropical regions--the total number of bacteria is 0.3-1.5•10^6 cl/ml, biomass 0.05-0.5 g/m^3 (Table 5). Production (based on the results of measurement by the radiocarbon method) in open waters in the summer averages 0.1-0.3, in the neritic zone--0.3-1 g/m^3 per day. The P/B coefficient of bacterioplankton is usually 0.3-0.6.

In oligotrophic surface waters--the trade wind currents in the oceans and eddy regions--the total number of bacteria decreases to 50-150•10^3 cl/ml, the biomass--5-50 mg/m^3 (Sorokin, 1964, 1971a, 1973c; Novozhilova et al., 1970; Strickland, 1971; Hobbie et al., 1972). Production is usually 5-30 mg/m^3 per day, the P/B coefficient is high--1-2.

In stratified oceanic basins, there are several maxima of concentration of bacterioplankton: in the surface film, over the thermocline and in the upper boundary of the intermediate Antarctic waters. In these layers, the biomass and production of bacterioplankton are usually several times higher than the average values we have presented (Sorokin, 1971a, c, 1974) (Fig. 13).

In cross sections from the shore into the ocean, the biomass and production of bacterioplankton in the surface layer both decrease rapidly (Fig. 14). The enriching influence of the shelf off small islands stops at a distance of only a few miles from the shore (Sorokin, 1973b). In the water deeper than the euphotic zone, the population, biomass and production of bacteria decrease rapidly with depth. Excluding the layer of the maximum at the upper boundary of the intermediate Antarctic waters at a depth of 450-550 m, the mean values of total population of bacteria deeper than 200 m drop to 2-6•10^3 cl/ml, of biomass to 0.2-0.8 mg/m^3, 10-20 times less than at the surface. The production of bacteria in the deep and intermediate waters decreases still more--by a factor of 50-100, to 0.01-0.05 mg/m^3 per day. In the layer of the maximum, at a depth of about 500 m, these quantities are 5-10 times higher (Sorokin, 1971a, c, 1973c, 1974).

These values of number and biomass of bacterioplankton were obtained by the method of direct microscopy. Measurement of the wet biomass of bacteria in the deep waters by the ATP method yields 2 to 5 times higher values (Holm-Hansen, 1969; Lyutsarev et al., 1975). The reasons for the difference should be sought, apparently, in the fact that these values of biomass are at the boundary of sensitivity of the ATP method and cannot be determined by this method with sufficient reliability. Also, the ATP method yields the actual biomass of all

Table 5. Mean population (N, c ·10^9/m), wet biomass (B, mg/m^3) and daily production (P, mg/m^3, wet mass) of phytoplankton and bacterioplankton (Sorokin, 1964-1974; Sorokin et al., 1975)

Basin	Biotope	Phytoplankton		Bacterioplankton			
		B	P	N	B	P	P,B
Black Sea (Summer)	Euphotic zone (av.)	50- 100	20- 40	40- 80	8- 20	10- 30	0-1.5
	Chemosynthesis zone, 150-170 m (max.)	---	---	200- 400	100- 200	40- 80	0.4-0.6
	Deeper waters, 300-2000 m (av.)	---	---	4- 10	2- 4	0.1	0.5
Sea of Japan (Summer)	Euphotic zone (av.)	50- 100	100- 1500	150- 300	100- 200	40-100	0.4-0.6
	" (max.)	200- 400	100- 300	1000-2000	600-1000	200-400	0.4-0.6
Tatar Bay (Summer)	" (av.)	700-1500	300- 600	1000-3000	500-2000	300-700	0.3-1.0
Peruvian Upwelling	" (av.)	300-1500	1000- 5000	600-1000	200- 500	100-300	0.3-0.8
	" (max.)	1500-5000	5000-12000	1000-5000	500-2000	200-400	0.2-0.5
Tropical coral shoals	" (av.)	100- 300	100- 1000	300-1500	300- 800	100-300	0.3-0.6
Equatorial divergence in the Pacific	" (av.)	300-1000	200- 1000	200-1000	100- 400	100-300	0.3-1.0
Pacific trades	" (av.)	10- 30	20- 50	50- 150	10- 30	20- 50	1 -3
	" (max.)	40- 100	50- 100	300- 600	60- 200	40-120	1 -1.5
	Intermediate Antarctic waters (av.)	---	---	10- 20	2- 6	0.5- 3	0.2-0.5
	" (max.)	---	---	50- 200	10- 40	5- 20	0.3-0.8
	Deep waters (av.)	---	---	2- 6	0.2-0.8	0.04-0.1	0.1-0.2

Note: av. = values outside maximum layer; max. = values in layer of mean maximum.

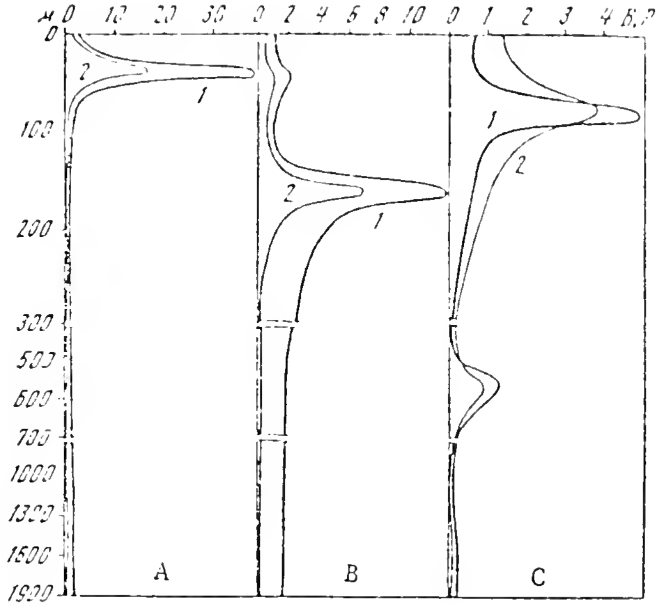


Fig. 13. Vertical distribution of microflora in the Sea of Japan (A), Black Sea (B), Pacific Ocean in the region of the southern trades (C): 1, biomass of bacterioplankton (B, mg C/m^3); 2, daily production (P, mg C/m^3).

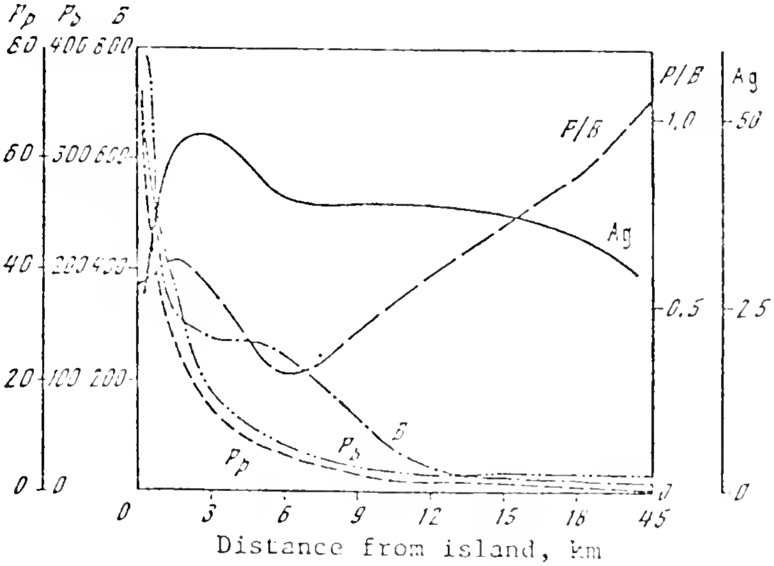


Fig. 14. Distribution of biomass (B, mg/m^3), daily production (P_b, mg/m^3) and daily P/B coefficient of bacterioplankton, primary production of phytoplankton (P_p, mg C/m^3 per day) and fraction of aggregates in bacterioplankton (Ag, %) in a cross section from Heron Island, Great Barrier Reef, Australia, in the direction of the open sea.

living matter, not of bacterioplankton as such. The decrease of biomass and activity of microflora in the deeper waters of the pelagic zone of the ocean, indicated by the ATP method, direct counting and assimilation of labeled CO_2, coincides with the results of the plate counts of heterotrophs (ZoBell, 1946) and measurement of the rate of consumption of ^{14}C-labeled organic matter by bacterioplankton in samples of deep water (Sorokin, 1970b; Takahashi, Ichimura, 1971).

One significant peculiarity of marine bacterioplankton is the clustering of a significant fraction (20-30%) of the microbial cells into aggregates (Jones, Jannasch, 1959; Sorokin, 1970a; Seki, 1971). The formation of aggregates measuring more than 5 μm in diameter is not a result of the absorption of bacterial cells on the surface of suspended particles, but rather a result of the growth of films or floccules of microcolonies. Their growth is independent of the presence of suspended particles in the water and continues to occur after aggregates already formed are filtered out (Sorokin, 1971a). The formation of organic aggregates under the influence of air bubbles described by Riley (1963b) does not occur in sterile water (Barber, 1966) and, consequently, is a result of bacterial activity. The aggregation of bacterioplankton is of important ecologic significance, since it assures that a significant fraction of the bacterioplankton will be accessible to coarse filter feeders such as the calanoids, which dominate in the populations of the pelagic mesozooplankton.

2.3 Microflora of the Bottom Sediments

The population density of bacteria in the upper layer of the bottom sediment varies as a function of the level of productivity of the region and of depth (Table 6). In the richest sediments of the shelf, the microflora composes as much as 4-6% of the organic matter in the sediment. The maximum values of total population, defined by the method of direct microscopy, is $1\text{-}9 \cdot 10^9$ cl/ml of wet sediment, which was found in shallow eutrophic regions: the lagoons of atolls, the littoral zones of inland seas (Butkevich, 1938; Salmanov, 1968; Novozhilova et al., 1970; Sorokin, 1970c, 1971b, 1973d). The production of bacteria in the sediments of such regions amount to 0.2-1 g/l of wet sediment, the P/B coefficient is 0.2-0.4. These data indicate the great intensity of the productive activity of microflora in the sediments of the shelf zone, assuring their high food value for the benthic invertebrates. It is not by chance that in this zone, a significant fraction of the benthos consists of silt swallowers.

In deep-water regions of the inland seas and on the continental slopes of the temperate and tropical regions of the ocean, the total number of bacteria in the surface layer of the soil is $0.2\text{-}1.10 \cdot 10^9$ cl/ml, their biomass is 0.1-0.4 g/l, their production--5-50 mg/l per day (Sorokin, 1964, 1970, 1971c; Anderson, Meadows, 1969; Seki, ZoBell, 1967; Salmanov, 1968; Ernst, 1970). In the bottom sediment in deep-water areas of the ocean--the radiolarian and pellitic silts and deep-water clays--the total number of bacteria decreases to $10\text{-}50 \cdot 10^6$ per ml, the biomass--to 3-30 mg/l, production--to 0.1-1 mg/l per day. The P/B coefficient is quite low--0.01-0.1.

Table 6. Number (N), biomass (B), and production (P) of bacteria in bottom sediments of the marine basins, per ml of wet silt (Sorokin, 1973c).

Location of Sampling Station, Type of Sediment	Depth, m	N, 10^6 cl/ml	B (wet weight), μg/ml	P, μg/ml·day
Pacific Ocean				
Fanning Atoll, coral sand	2	2030	910	226
Majuro Atoll, periphyton on dead coral	3	6200	2480	2150
Slope opposite Tokyo Bay, silty-sandy stone	2725	196	94	13
Near equator, diatom-radiolaria silt	5020	37	17	1.4
Northern trades, red clay	5810	14	6.6	0.6
Southern trench, red clay	5330	7	3.4	0.03
Sea of Japan				
Yamato Bank, aleuritic-pelitic silt	70	1.54	175	120.0
West coast shelf, aleuritic silt	100	0.41	98	4.5
Central trench, aleuritic-pelitic silt	2000	0.18	25	0.2
Black Sea				
Central trench, aleuritic-pelitic silt	2000	0.98	250	3.2
Slope, aleuritic silt	300	2.96	750	56
	180	4.91	2600	48

The distribution of the benthic microflora in the deep-water regions (Table 6) show that its biomass depends on the level of productivity of the region (Sorokin, 1970c). These observations disagree to some extent with the conclusion of independence of the quantity of suspended organic matter in deep waters of the productivity of the surface waters (Menzel, 1967). This contradiction may be explained by the fact that the primary source of organic matter in the bottom sediment is not dispersed suspended matter, but rather the remains of planktonic organisms, the number of which is directly dependent on the level of productivity of the surface waters. These remains, as well as their faeces, may reach the bottom of the deep ocean in 5-15 days (Saunders, 1969).

2.4 Microflora of Detritus of Periphytonic Fouling

Detritus is formed as a result of the destruction of the remains of dead organisms and the excrement of microflora and protozoa. During the course of this processing in organic aggregates, which make up the mass of detritus, a unique type of microcommunity is formed, consisting mostly of bacteria, infusoria and heterotrophic flagellata, as well as algae (primarily diatoms), and even small crustacea (Rodina, 1963; Fenchel, 1970). They determine the food value of the detritus, which serves as one of the main sources of nutrition of planktonic and benthic filter feeders, particularly in the highly productive areas of the shelf and in the water beneath the eutrophic zone (Odum, de la Cruz, 1963). In "young" detritus particles, the source of energy for bacterial biosynthesis is the substance of the dead remains itself, while in "mature" detritus particles, it is the dissolved organic matter of the sea water (Finenko, Zaika, 1970; Khaylov, 1971). As a result of bacterial biosynthesis utilizing this external organic matter, the mass of organic matter in the detritus may increase as it matures, as is observed, for example, in the feces of shrimp, which was held for several days in sea water (Johannes, Satomi, 1966).

The total population of bacteria in the detritus and detrital sediments reaches magnitudes comparable to those of the active silt in sewage plants: $5\text{-}25 \cdot 10^9$ cl/ml. The mass of bacteria represents as much as 4% of the total organic matter of the detritus (Rodina, 1963; Fenchel, 1970, 1972; Sorokin, 1971b; DiSalvo, 1973). The intensity of the metabolism of detritus (20 mg O_2/g·day) is close to that of the benthic animals of the same weight. Thus, detritus must not be considered dead organic matter: actually, it is an active component of the ecosystem. It is the living fraction of the detritus which is assimilated as it is consumed by filter feeders and sestonophages (Newell, 1965; Sorokin, 1971b, 1972; Hargrave, 1971; Fenchel, 1972; Odum, 1975).

The porous surfaces of rocks, dead corals, clastic material, and particles of large-grained benthic sediment are abundantly overgrown with periphytonic microflora (Khaylov, Gorbenko, 1967; Sorokin, 1971b, 1973d). The biomass of bacteria in the periphyton on dead coral is 2-5 mg/g of scrapings. A significant portion consists of filamentous forms of flexibacteria such as Cladotrix, Crenotrix, or Leucotrix. The latter frequently cover the surface of dead corals and the periphytonic algae growing on it in a solid layer. Bacterial foulings on dead corals, fragments, and large-grained sediment in coral reefs is one of the most metabolically active components of the ecosystem and the primary nutrient component of periphyton, consumed by many benthic animals.

2.5 Biogeochemical Activity of Marine Microflora

In aerobic marine basins, the basic biogeochemical functions of the microflora is the oxidation of organic matter and the creation, by means of the energy liberated in this process, of their own biomass. The processes of biochemical consumption of oxygen and formation of CO_2, regulating the content of oxygen, pH and Eh of sea water and sediments are related to these large-scale biogeochemical processes performed by the microflora; the regeneration of inorganic forms of nitrogen and phosphorus during the course of oxidation of organic matter by microflora; the oxidative transformation of ammonia and urea into nitrates; the fixation of atmospheric nitrogen, achieved by the energy of oxidation of organic matter; processes of regulation of the content of dissolved organic matter (DOM) and suspended organic matter in sea water by the activity of microflora inhabiting the surfaces of suspended particles (DOM-suspension system); accumulation and precipitation of biologically active metals (Fe, Mn, Co, certain trace elements) after they are included into the bacterial biomass and subsequently introduced into the food chain; the synthesis of organic forms of phosphorus and nitrogen from inorganic forms upon oxidation of organic matter by the microflora.

Let us analyze the available data on the intensities and mechanisms of these processes.

2.6 Intensity of Microbial Decomposition of Organic Matter and Consumption of Oxygen in the Water and in Sediments

The total concentration of organic matter in the water of the ocean is 1.5-2.5 mg C/l, or about 15 kg/m^2 of dry organic matter. About 60% of this matter is represented by the relatively stable fraction of aqueous humus (Skopintsev, 1966; Ogura, 1972), the remainder--by low-molecular components: amino acids, fatty acids, carbohydrates (Duursma, 1965; Khaylov, 1971; Andrews, Williams, 1971). The absolute content of organic matter, its composition, the content of the available fraction of DOM and suspended matter, determined by the potential BOD (biochemical oxygen demand) or the potential production of bacteria (Fig. 15), change relatively little right up to very great depths (Novoselov, 1962; P. M. Williams, 1969; Starikova, Korzhikova, 1970; Finenko, Ostapenya, 1971; Sorokin, 1971a,d,g; Menzel, 1978). These data contradict the traditional concept of the predominance of inert aqueous humus at great depths, which was set forth at one time to explain the extremely low BOD in the deep waters of the ocean. It was based on the concept that the source of replenishment of organic matter in the deep water consists of the remains and excrement of the plankton sinking down from the higher layers.

According to modern concepts, the deep and intermediate waters are formed of productive surface waters descending at the convergences in the high latitudes, then drifting in the direction of the equator. In the zones of the tropical divergences, they rise and are redistributed by the equatorial currents (Stommel, Aarons, 1960; Veronis, 1972). In accordance with this model, the main path of penetration of organic matter into the deep and intermediate waters is its horizontal transfer from the productive high-latitude regions (Redfield, 1942; Wyrtki, 1962). This mechanism explains fully a relative uniformity of distribution of organic matter in the water column described earlier. The low actual values of BOD are explained not by the great stability of organic matter in the deep waters (which has not been confirmed by recent studies), but rather by the unfavorable conditions for the functioning of deep-water microflora; the joint inhibiting effect of low temperature and high pressure (Sorokin, 1969, 1971c; Jannasch et al.,

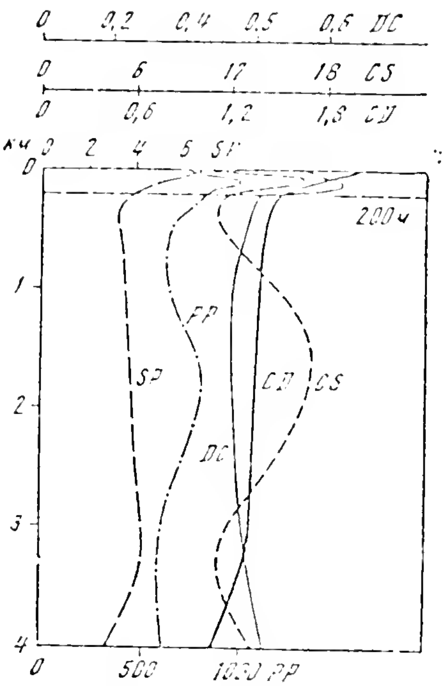


Fig. 15. Vertical distribution of organic matter (DOM) in the water of the Western Pacific: CD, total content of DOM (mg C/l); CS, organic carbon in suspension (μg/l); DC, dissolved carbon (μg C/l), data of Ye. A. Romankevich; PP, potential production of bacteria (mg C/m^3).

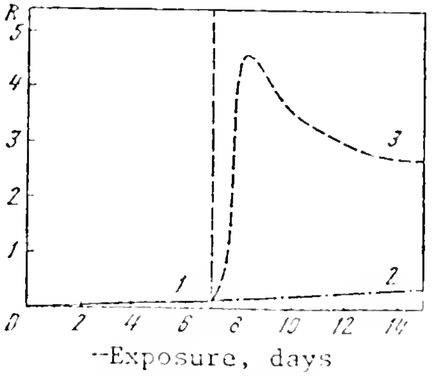


Fig. 16. Rate of assimilation by bacterioplankton (4°N, 135°W) of the labeled protein hydrolysate injected into a sample of sea water at moment of closing of a water bottle at 4000 m depth after its subsequent exposure at this depth for 7 days (1), then in the laboratory at 2°C (2) and on the deck at 30°C (3). Initial concentration of hydrolysate in samples 0.3 mg/l, initial radioactivity .2 10^6 pulses/l. R = radioactivity of bacterioplankton, 10^4 pulses/100 ml.

1971). Experiments have shown that the bacterial activity in deep samples (from 3000-4000 m) upon exposure of the samples in situ, is low even when the samples are enriched with easily assimilated organic matter (Fig. 16).

The rate of biochemical decomposition (respiration) in deep waters, expressed in units of oxygen consumed, according to the results of physical and chemical calculations (Riley, 1951; Munk, 1966; Arons, Stommel, 1967) and measurements of the concentration of ATP and ETS (electron transport enzymes) in the plankton yield values of decomposition in deep waters of 0.01-0.06 mg O_2/m^3 per day (Strickland, 1971; Hobbie et al., 1972). This rate of destruction corresponds to an oxygen consumption of 0.1-0.2 mg/l yr. With this rate of destruction, the reserve of oxygen in descending Antarctic waters should be sufficient for 50-100 years.

Direct analyses of the intensity of the destruction in the "old" deep waters in the central part of the Pacific by the ^{14}C method have yielded quantities close to the calculated quantities (Table 7). In the deep waters of the Western Pacific, where, according to the model of global circulation (Kuo, Veronis, 1970) the primary flow of meridional advection of Antarctic water occurs, the values were 3 to 6 times higher (Sorokin, 1971a). In the upper layer of the intermediate Antarctic waters at depths of 400-800 m, the values of destruction, according to ^{14}C and ATP data, increase to 3-5, in the layer of the bacterial maximum at a depth of 500-550 m- to 10-20 mg O_2/m^3 per day. With this intensity of destruction, we should see a shortage of oxygen at this level within 1-2 years, which does actually occur (Fig. 17). These data indicate that the shortage of oxygen ordinarily observed in intermediate waters is formed primarily as a result of local consumption of O_2 by microflora which have a constant maximum of activity here.

The rate of decomposition in the surface waters of the pelagic zone of the oceans is 20-30 mg O_2/m^3 per day in oligotrophic waters, 50-200 mg O_2/m^3 per day in mesotrophic and eutrophic waters.

Determination of the potential destruction (long-term exposure of samples at 20-30°C) by the ^{14}C and BOD methods yield values of 0.15 mg O_2/l, both in deep and in surface samples (Sorokin, 1971a, 1973c; Novoselov, 1962). The BOD rate constant in surface waters of the ocean is 0.02-0.10, close to the constant of the rate of destruction of phytoplankton in sea water (Skopintsev, 1966; Finenko, Ostapenya, 1971; Ogura, 1972).

The rate of bacterial destruction of organic matter in the bottom sediments of the seas can also be characterized by the rate of oxygen consumption, since biologic oxidation of organic matter in sediment, performed primarily by microflora, significantly predominates over chemical oxidation. The rate of destruction of organic matter in bottom deposits, based on averaged data for various biotopes and the integral values of destruction beneath each square meter in a layer 5 cm thick (considering the nature of distribution of bacterial activity in the sediment) are presented in Table 8. In the sediment of the neritic zone, 1 g of silt absorbs about 0.1 mg O_2/day. The annual destruction

Table 7. Mean biochemical oxygen demand (BOD, mg O_2/m^3 per day) in waters of the ocean, and as determined by various methods (Riley, 1951; Novoselov, 1962; Munk, 1966; Arons, Stommel, 1967; Pomeroy, Johannes, 1968; Holm-Hansen, 1969; Sorokin, 1971a; Ostapenya, 1971; Strickland, 1971, and others).

Biotope	Temperature	^{14}C Method	Other methods*
Subarctic surface water	1-3	--	4 (b)
Shelf water from boreal zone	18	250	300 (b)
Surface water of boreal zone	16	80	100 (b)
Tropical water of coral shoals	30	200	400 (b)
Tropical surface water of coastal upwelling	19	150	240 (ATP), 190 (b)
Tropical surface water of equatorial divergence	25	70	50 (ATP), 60 (b)
Tropical surface water of western pelagic zone	28	25	70 (b, BOD)
Tropical surface water of central ocean	27	20	40 (b, BOD)
Intermediate Antarctic water of central ocean	6-8	5	3 (ATP, b)
Deep water of western part of ocean	2-4	0.3	0.3 (b)
Deep water of central region of ocean	2-4	0.4	0.2 (ATP, TP), 0.1 (b, TG)

*Methods: b = measurement of oxygen consumption in bottles in short-term or long-term experiments; ATP = calculation on the basis of the content of ATP in plankton using the ratio BOD:ATP = 500; TP = theoretical calculation on the basis of physical data; TG = theoretical calculation on the basis of geochemical data.

in these sediments is about 200 g O_2/m^2. The oxygen shortage caused by this intensive consumption in the sediment of the neritic zone is largely compensated for by its liberation upon photosynthesis by the periphyton and phytobenthos. Due to the intensive destruction occurring in the bottom sediments in the neritic zone and shelf, about 20% of the total primary production is decomposed by the bottom microflora.

The bottom sediments of the slopes are also characterized by rather intensive metabolism of their microflora: up to 40 μg O_2/day, or 30-60 g O_2/g of sediment. The intensive metabolism of the microflora in the sediment on the slopes is a result of the high rates of sediments accumulation and the rapid delivery of fresh organic matter from the shelf as the upper layer of sediment flows down the slope.

Table 8. Rate of destruction in benthic sediment of the world ocean (Ryther, 1969; Hayes, 1964; Sorokin, 1970)

Zone	Depth, m	Area, $km^2 \cdot 10^6$	Annual Production of Photosynthesis in water over zone (P_p), 10^9 t C	Annual Production of Bacteria in upper layer of sediment in area of zone, 10^6 t C	Destruction				Q/P_p, %
					$\mu g\ O_2/cm^3 \cdot day$	$\mu g\ C/cm^3 \cdot day$	$g\ C/m^2 \cdot yr.$	Destruction in area of zone (Q), 10^6 t C/yr.	
Interior Shelf	0- 50	13	3.9	185.0	107.0	40.0	72.0	935	24
Exterior Shelf	50- 200	18	2.7	97.0	40.0	15.0	27.0	485	18
Slope	200-1000	15	1.5	10.8	10.7	4.0	7.20	108	7.2
Slope foot and deep water plains	1000-4000	106	6.7	11.6	0.66	0.2	0.45	48	0.7
Deep central parts of oceans	4000-5000	208	10.4	3.1	0.26	0.1	0.18	37	0.35
Total	---	306	25.2	307.5	---	---	---	1613	6.5*

* Mean value

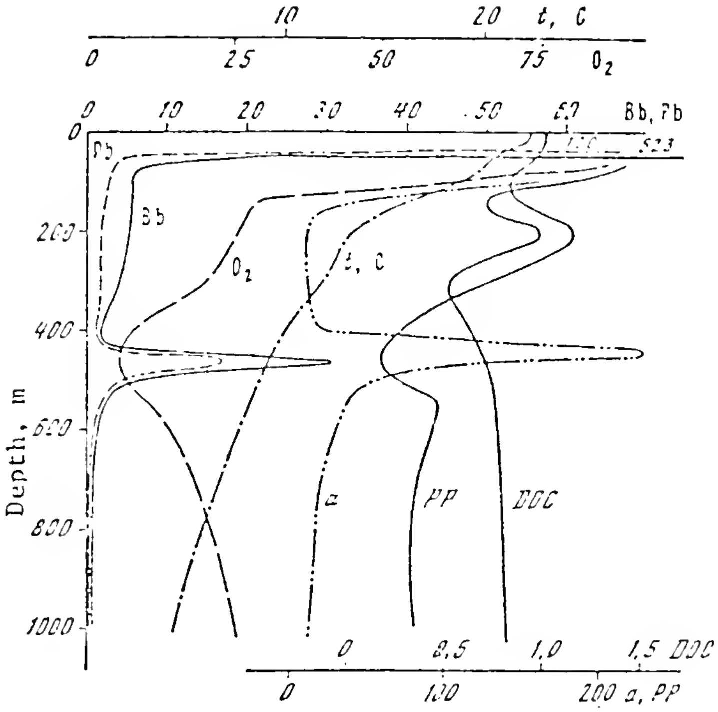


Fig. 17. Vertical distribution of bacterioplankton and environmental factors in the region of the equatorial divergence in the eastern Pacific (01°S, 97°W). Bb and Pb = biomass and daily production of bacteria (mg/m^3); a - relative activity of heterotrophic bacteria; PP - potential production of bacteria (mg/m^3); DOC - dissolved organic carbon (mg C/l); O_2 - dissolved oxygen (% of saturation); t, C - temperature.

In deep-water sediments of the pelagic zone, the intensity of destruction decreases by 2 orders of magnitude, to 0.2-0.5 μg O_2/m^3. Only about 0.3% of the primary production of pelagic zone is destroyed in these sediments.

Calculations on the basis of data on the total destruction of organic matter in benthic sediment of the ocean yields a value of 1.6 10^9 t of carbon, or about 6% of the global primary production. This level of global primary production is based on studies by the radiocarbon method, but if we consider that the value produced by this method is probably low by a factor of 3 or 4, the actual fraction of primary production which is destroyed in the benthic sediment should be estimated as 1.5-2%.

Data on the intensity of bacterial production and destruction, the coefficients of specific production of marine microflora and the variation in the intensity of metabolism with temperature in situ (Sorokin, 1969, 1970d,e, 1971a,g, 1973c,d) allow calculation of the approximate total values of destruction of organic matter, bacterial biomass and production in the ocean (Table 9). In the calculations, we used the relationship between daily bacterial production (P, mg C/m^3) and destruction (D, mg O_2/m^3): P = 0.08 D (Sorokin, Kadota, 1972). The total bacterial production of organic matter in the World Ocean is over $2 \cdot 10^{10}$ t of carbon with a total biomass of the microflora of $0.23 \cdot 10^9$ t. The predominant part of bacterial production (over 60%) is created in the warm surface waters between 20° N and 20° S at 20°-28°C. This explains the relatively high mean daily P/B coefficient for the microflora of the World Ocean--0.35.

In the high latitudes, bacterial processes in the organic matter cycle are inhibited by the low water temperature. Only about 2% of the total bacterial production is created in these waters. The bacterial production and, consequently, destruction of organic matter in the benthic sediment represents only about 1.5% of their values in the water, since most of the ocean floor (over 80%) consists of deep-water sediment with little content of organic matter, where the metabolism of the microflora is inhibited by the high pressure and low temperature.

The total annual destruction of organic matter in the World Ocean is near $2.5 \cdot 10^{11}$ t O_2, or $8 \cdot 10^{10}$ t carbon (respiratory coefficient 1.2). This quantity in principle should be close to the primary production of organic matter by microflora. However, a comparison of this quantity with the primary production in the World Ocean, based on theoretical calculated values of oxygen consumption (Skopintsev, 1967) or measurements by the radiocarbon method (Koblentz-Mishke et al.,1968) shows that consumption is only one-third of the values of destruction presented above. This disagreement is most probably a result of the generally recognized fact that the values of primary production determined by the radiocarbon method is underestimated (Arthur, Rigler, 1967; Pomeroy, Johannes, 1968; Riley, 1972).

All of the errors of the radiocarbon method lead to lowering of the results (Sorokin, 1971a). These errors were particularly great during the first few years of application of the method (before 1960). The values produced at that time formed the basis for calculations of the total primary production of the World Ocean presently used for global estimates of productivity (Moiseyev, 1969; Ryther, 1969; Bogorov, 1974).

Calculation of the probable energy losses in the heterotrophic portion of the living population of the World Ocean indicate a necessary energy "input" to the ecosystem of $7.6 \cdot 10^{17}$ kcal/yr which is also three times the calculated value of primary production.

2.7 Participation of Microorganisms in the Cycling of Nutrients

The decomposition of organic matter by microflora and production due to the energy liberated in this process of bacterial biomass represent one of the basic mechanisms of the circulation of nitrogen and phosphorus in the sea. In the process of microbial decomposition the nutrients are regenerated. A great significance of biogeochemical regeneration of nutients results from the fact that photosynthesizing plants can consume largely their inorganic forms. Therefore, the rate of regeneration and of their transfer from zones of regeneration to the euphotic layer is a primary factor regulating the productivity of the oceans. The rate of

Table 9. Total values of bacterial destruction, production and biomass in the Pacific and world oceans (Sorokin, 1971g)

Region	Area, km^2·10^6	Daily Destruction			Daily Bacterial Production		Biomass of Bacteria		Mean daily Coefficient for water mass
		g O$_2$/m^2	For entire region, 10^6 t O$_2$	% of Sum	g C/m^2	For entire region, 10^6 t C	g C/m^2	For entire region, 10^6 t C	
Pacific Ocean									
60°-70° N	11.9	0.37	4.4	1.4	0.033	0.39	0.24	2.8	0.14
50°-60° N	13.1	0.56	7.3	2.2	0.053	0.69	0.37	5.0	0.13
40°-50° N	12.1	0.89	10.8	3.4	0.083	1.00	0.39	4.7	0.21
20°-40° N	26.2	1.88	50.1	15.7	0.175	4.60	0.63	16.4	0.28
20°-20° N-S	63.2	3.05	194.0	61.0	0.286	18.30	0.82	52.0	0.35
20°-40° S	21.8	1.97	43.2	13.5	0.184	4.00	0.65	14.2	0.28
40°-60° S	16.9	0.71	12.2	3.8	0.067	1.14	0.32	5.4	0.21
Entire ocean, per day	165.2	--	322.0	100	--	30.10	--	100.5	--
Entire ocean, per year	165.2	--	11.7·10^4	--	--	1.1-10^4	--	--	--
World Ocean									
In water, per year	360.0	--	25.2·10^{10}	--	--	2.4·10^{10}	--	226	--
Bottom sediment, per year	360.0	--	0.43·10^{10}	--	--	0.03·10^{10}	--	1.8	--

regeneration, on the average, is proportional to the indices of destruction rate, such as the BOD (Redfield et al., 1963). Microorganisms have no monopoly on the regeneration of nutrients. Other heterotrophs also take part in the destruction of organic matter. Their share in this process generally corresponds to the share of their participation in the destruction of organic matter, or the fraction of the total energy flow which they expend. There are rather stable relationships between the respiration of zooplankton and the quantity of mineral forms of nutrients which they liberate: they average 80 for phosphorus, 20 for nitrogen (Conover, Corner, 1968). These values in this case are significantly lower than the stoichiometric relationships with total oxidation of matter by phytoplankton, which is related to the selective assimilation of nutrient enriched substances and their incomplete oxidation by zooplankton. During bacterial oxidation of organic matter in sea water which is poor in nitrogen and phosphorus, these relationships may also be lower than the stoichiometric values, particularly since a significant portion of the nutrients is consumed by the bacteria themselves for biosynthesis. The consumption of inorganic nutrients by bacterioplankton in some biotopes makes the bacterioplankton a serious competitor for the phytoplankton. This occurs in surface tropical waters where, even within the euphotic zone, most of the inorganic phosphate is consumed by bacteria, but not by phytoplankton (Sorokin, Vyshkvartsev, 1974), since the microflora oxidizes primarily "old" organic matter, brought in from other regions of the ocean, which is poor in phosphorus.

The most important function of the microflora in the cycle of nutrients is that they can mineralize or assimilate biogens in such stable dissolved organic compounds as nucleic acids. In a number of biotopes, for example, in the surface tropical waters, the main stock of nutrients is in just these forms. Their inclusion in the metabolism of the plankton community can occur only through the process of biosynthesis of the bacterial biomass, which is then mineralized by the bacteria-consuming planktonic animals, primarily the ciliates and phytophagous Copepoda. It has been established that the ciliate, in a period of 5-15 minutes, liberate a quantity of mineral phosphate equal to its total content in the body. For the calanoids, this time is 5-10 days. The Protozoa, in spite of their relatively low biomass, apparently play a leading role in the mineralization of the biogens in the organic matter of the bacteria and phytoplankton (Johannes, 1964, 1968), since the Protozoa perform a significant fraction of the total metabolism of the community (see Fig. 12).

Studies of the vertical distribution of nitrates and phosphates, the content of organic phosphorus, O_2 and CO_2 in various regions of the ocean, have revealed regular changes in the relationship of their concentrations, which develop in the course of mineralization of the organic matter of the phytoplankton. Thus, the atomic ratio of nitrates to phosphates in the top 300 m of water is close to that in the cells of the phytoplankton--15:1 (Redfield et al., 1963). It has still not been established with certainty just where the processes of mineralization are located in the waters of the ocean (Menzel, 1970). The assumption which was earlier held, that processes of mineralization and related formation of the oxygen minimum occurred due to utilization of locally produced organic suspended matter, cannot explain the regularities of quasi-conservative distribution of phosphates and dissolved oxygen in the water which have been observed. Their distribution is related not only to local processes of mineralization, but also to the global oceanic circulation. The most acceptable solution is the assumption that processes of mineralization, leading to the generation of mineral phosphate and the formation of the oxygen minimum, occur in the intermediate Antarctic waters along the path from the region of their formation (at the Antarctic convergence) to the equator. The substrate of the destruction is the organic matter of the productive surface Antarctic waters descending in the zone of convergence (Wyrtki, 1962; Redfield et al., 1963). This plan is confirmed by data on the intensification of bacterial destruction at the upper boundary of the Antarctic waters (see Fig. 17). As we noted earlier, the intensity of the process of destruction is sufficient to form an oxygen minimum and result in regeneration of nutrients in 1-3 years.

The concentration of organic phosphorus in the surface topical waters of the ocean is 0.2-0.4 µg-atom/l, or 60-80% of the total phosphorus. Therefore, the processes of local bacterial mineralization of this reserve of nutrients, consisting primarily of the stable soluble fraction, are of geat significance in the provision of biogenic nutrition for the phytoplankton. Ammonia is formed as a result of mineralization of organic forms of nitrogen by bacteria. In regions where the surface waters are poor in nutrients, it is consumed by the phytoplankton before it is oxidized to nitrate. In oligotrophic tropical waters, up to 99% of the mineral nitrogen is utilized by the phytoplankton in the form of NH_4^+ (Dugdale, Goering, 1967). A portion of the ammonia nitrogen, formed as a result of mineralization, is oxidized to nitrites and then to nitrates by the nitrifying bacteria (Watson, 1963; Carlucci, McNally, 1969). It is presumed that the nitrates of the deep and intermediate waters are formed due to oxidation of ammonia in the regions of the high-latitude convergences, where they submerge with the descending waters (Dugdale, 1969).

2.8 Significance of Microbial Biosynthesis in the Cycle of Some Mineral Elements

A large-scale biogeochemical process of production of microbial biomass in the ocean involves carbon plus other elements, which are included in the composition of the protoplasm of the microorganisms: nitrogen, phosphorus, iron, trace elements. Data are presented above on the scale of involvement of inorganic phosphate into the bacterial synthesis. As concerns nitrogen, the situation should be similar, particularly with oxidation of organic matter by the microflora in deep waters and in bottom sediment, but this process is poorly studied. It has been shown that the marine microflora can cause nitrification and inclusion of molecular nitrogen into biosynthesis (Maruyama et al., 1970; Pshenin, 1966). However, it is very difficult to make a distinction between nitrification of bacteria and of blue-green algae. The total nitrification in the sea may exceed 300 g/ha•day (Dugdale, Goering, 1964).

Experiments involving the use of the radioisotopes of iron and cobalt have shown that iron is consumed by bacterioplankton at a rate of 0.5 µg per mg of organic carbon of the bacterial biomass produced. Cobalt is consumed by marine bacterioplankton for the synthesis of vitamin B_{12} in the proportion of 0.4 μg per mg of C_{org}. The bacteria producing this vitamin are quite common in the sea (Sorokin, 1971a; Lebedeva et al., 1971). It has been established that the consumption of cobalt by bacteria and its inclusion in this manner in the food chain is the main path by which cobalt arrives into the benthic sediments. This metal does not form insoluble hydroxides and enters the bottom sediment in significant quantities with the fecal matter of the invertebrates which feed on bacteria (Sorokin, 1972, 1973a,g). Based on analyses of the intensity of consumption of iron, manganese and cobalt by bacteria and phytoplankton, the time of total consumption of these elements by them has been calculated (Table 10).

Table 10. Calculation of probable time of consumption of the stock of dissolved iron, manganese and cobalt in the World Ocean by bacteria and phytoplankton.

Element	Annual assimilation, g		Total Assimilation, g/yr	Reserve in Sea Water, g	Time of Complete Assimilation, years
	Phyto-plankton	Bacteria			
Fe	$3.5\cdot10^{14}$	$4\cdot10^{12}$	$3.6\cdot10^{14}$	$1.4\cdot10^{16}$	40
Mn	$3.5\cdot10^{13}$	$4\cdot10^{11}$	$3.6\cdot10^{13}$	$1.4\cdot10^{15}$	40
Co	0	$3.2\cdot10^{12}$	$3.2\cdot10^{12}$	$7\cdot10^{14}$	220

2.9 The Trophic Role of Microflora in Marine Ecosystems

The concept of the significant role of bacteria in the food chains of aquatic communities was formulated and a basis provided for it by A. G. Rodina and S. I. Kuznetsov. They showed, primarily in qualitative laboratory experiments, that the trophic function of the bacterial population of bodies of water consists in the conversion of dispersed organic matter into the matter of microbial cells which are accessible as a food for invertebrates consuming bacteria. The continuation of investigations of the structure and functioning of marine ecosystems (Vinogradov, 1971) required extensive quantitative development of the problem of the trophic role of bacteria, in order to evaluate the fraction of microflora in the transformation of organic matter and energy and the formation of the food resources of marine ecosystems. Studies performed on board the VITYAZ' and AKADEMIK KURCHATOV in 1968-1974, allowed methodologic approaches to be developed to the solution of this problem and certain preliminary data to be obtained.

A quantitative estimate of the significance of microflora in the food chains of marine ecosystems requires information on the concentrations of bacterial biomass and the rates of its production, the sources of energy for bacterial production and the characteristics of effectiveness of nutrition of massive species of invertebrates by bacteria. The results of the studies of the feeding of planktonic and benthic invertebrates, performed using ^{14}C in field conditions as well as in basic laboratories, showed that natural bacterioplankton can serve as a normal source of nutrition for infusoria, sponges, hydroids, coral polyps, Appendicularia, planktonic crustaceans (Cladocera, copepods, euphausiids), bivalves and gastropods, filtering polychaetes (sabellids, and serpulids), holothurians, ascidians (Sorokin, 1966, 1971b, 1972, 1973a,d,e; Sorokin et al., 1970; Pavlova, Sorokin, 1970; Pavlova et al., 1971; Petipa et al., 1971, 1974; Ponomareva et al., 1971). Figure 18 presents the results of determination of the comparative intensity of nutrition of a number of filter feeders by phytoplankton and bacterioplankton.

For the fine filter feeders (sponges, Appendicularia, Cladocera, Polychaeta, veligers, mollusks), bacterioplankton at concentrations close to the natural ones (0.2-1 g/m^3 wet biomass) can fully satisfy their nutrient needs. For many of these species, they are an even more important source of nutrition than the phytoplankton. The coarse filter feeders (copepods, euphausiids, bivalve mollusks, ascidians) are unable to filter out the dispersed bacterial cells and consume primarily the aggregated portion of the bacterioplankton. They, therefore, use bacterioplankton less effectively than phytoplankton of the same concentration (Fig. 19). Nevertheless, for them also, the microbial biomass is an important reserve of additional food. In experiments involving determination of the intensity of consumption of labeled bacterioplankton by coarse filter feeders (Copepoda), with the same concentration of unlabeled phytoplankton present, and vice versa (Petipa et al., 1974), it was shown that the bacterioplankton represented 30-50% of their diet (Fig. 20). Even such predacious crustaceans as Euchaeta marina frequently consume bacterioplankton.

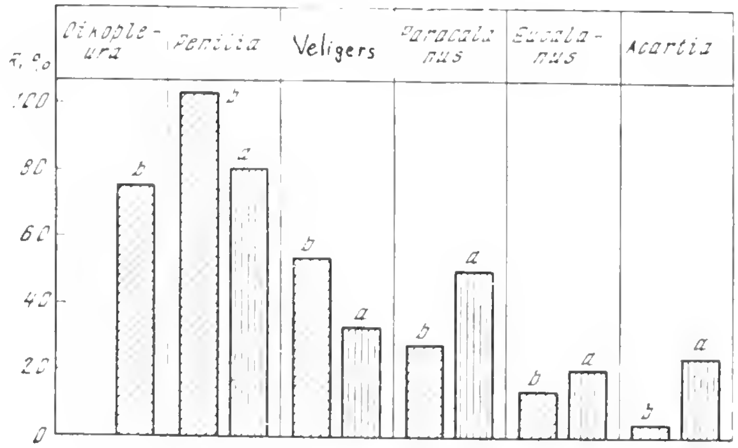


Fig. 18. Daily rations (R, % body weight) of massive species of plankters and their nutrition by bacterioplankton (a) and phytoplankton (b). Fine filter feeders (Oikopleura, Penilia), the veligers (Serpulorbis), medium filter feeders (Paracalanus), coarse filter feeders (Eucalanus), and predators (Acartia).

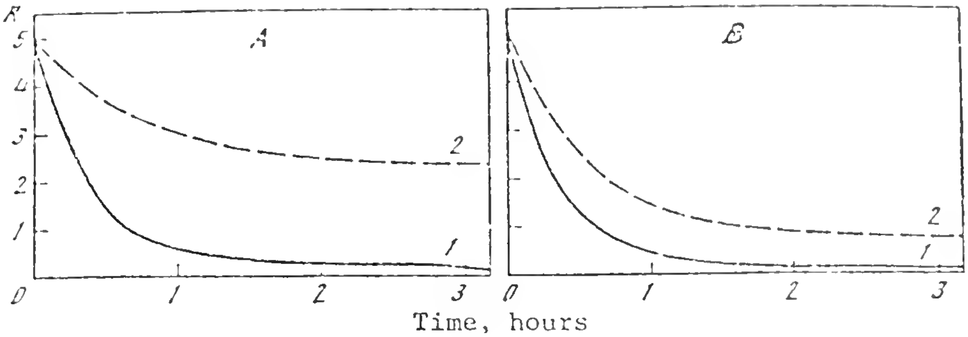


Fig. 19. Consumption of natural ^{14}C-labeled bacterioplankton containing cell aggregates (B) and the same bacterioplankton with aggregates filtered out by a membrane filter (A) by a fine filter feeder--the sponge *Toxadocea violacea* (1) and a coarse filter feeder--the oyster *Crassostrea gigas* (2): R = radioactivity of labeled bacteria in water, 10^3 desintegrations per minute/20 ml.

Using the ^{14}C-labeled bacterioplankton, the optimal concentrations of bacterioplankton for the nutrition of coarse and fine filter feeders were determined (Fig. 21). For the coarse filter feeders, the optimal concentration of bacterioplankton is that at which the bend occurs in the corresponding curves, at 1-1.5 g/m^3. These values are characteristic for littoral eutrophic marine biotopes or the layers of maximum concentration of plankton in highly productive upwelling zones (see Table 5). In these waters, even coarse filter feeders can supply their nutritional needs by eating bacterioplankton. For fine filter feeders, the optimum concentration is 0.2-0.4 g/m^3. These concentrations are found in the layers of maximum concentration in boreal waters in the summer, the neritic waters of boreal and tropical areas, and the pelagic zone near the tropical divergences. Thus, over a significant portion of the ocean, fine filter feeders can fully satisfy their nutritional needs by means of bacterioplankton alone.

The bacteria are assimilated to 40-60%, close to the level of assimilation of phytoplankton (Sorokin, 1968; Sorokin et al., 1970; Pavlova, Sorokin, 1970; Pavlova et al., 1971; Petipa et al., 1974). The daily rations of fine filter feeders with small body size, such as the veligers, *Appendicularia*, Cladocera, hydroids when feeding on bacterioplankton amount to 50-100% of their body weight. The daily expenditures of these animals for metabolism amount to 15-20% of their body weight. Therefore these animals can compensate for the metabolic expenditures by feeding with bacteria at their concentration 3 to 5 times less than the optimal (Pavlova, Sorokin, 1970). For example, for the Black Sea cladoceran *Penilia avirostris*, the threshold concentration of food at which the crustacean can compensate for its metabolic loss was found to be only 50 mg/m^3, significantly lower than the biomass of bacterioplankton in the littoral zone.

Special studies of the role of bacterial nutrition have been undertaken for bottom filter feeders of the tropical shelf. These

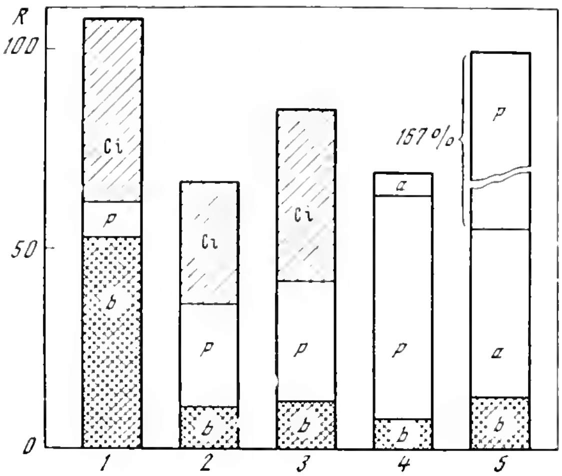


Fig. 20. Importance of various food sources in the formation of the diet of some common species of mesoplankton in the area of the equatorial divergence in the Pacific Ocean: R - daily ration (% of body weight); b - bacterioplankton; P - phytoplankton; Ci - ciliates; a - animal food (mixture of small calanoids); 1 - Clausocalanus sp.; 2 - Paracalanus parvus; 3 - Undinula darwini; 4 - Eucalanus attenuatus; 5 - Acartia clausi; (Petipa et al., 1975).

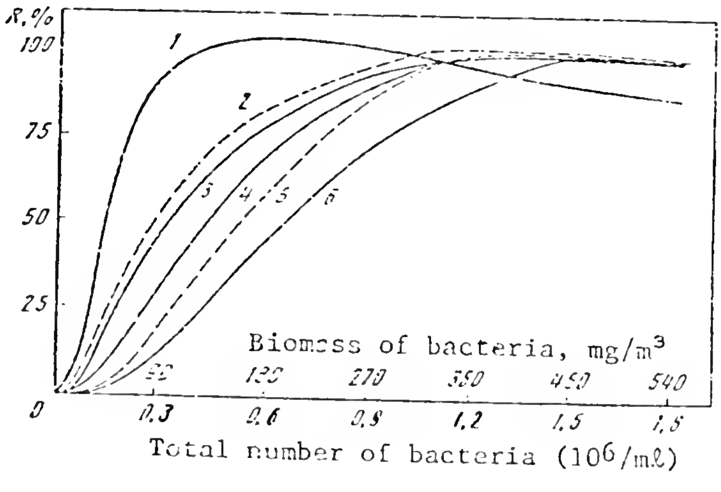


Fig. 21. Variation of intensity of nutrition (R, %) of some mass species of marine invertebrates with bacterioplankton as a function of its concentration: 1 - the sponge Toxadocea; 2 - the veligers Vermetidae; 3 - the polychaete Megalomma; 4 - the coral Pocillopora; 5 - the oyster Crassostrea; 6 - the copepoda Eucalanus.

experiments showed that oysters, polychaetes, sponges and ascidians are capable of normal feeding on bacterioplankton at its natural concentration. Their nutrition in this case is no less than it would be if they fed on fine phytoplankton. The filtering rate was 200-600 l/g of organic carbon in the body of the animals per day. It was found that coral polyps can also consume bacterioplankton (Sorokin, 1972, 1973a, b, e). The capability of coral to digest the bacteria they consume was proven by measuring the radioactivity of CO_2 liberated by them after feeding on labeled bacteria.

One important intermediate trophic link allowing the utilization of bacterioplankton in the food chain are the Protozoa: the ciliates (Tintinnidae, Strombidium) and the colorles flagellates such as Bodo (Fenchel, 1970; Fenchel, Reidl, 1970; Johannes, 1965; Petipa et al., 1974). The protozoans consume bacteria and themselves serve as food for the crustacean micro- and mesozooplankton (Mordukhay-Boltovskaya, Sorokin, 1965; Monakov, Sorokin, 1971; Pavel'yeva, Sorokin, 1971). In the boreal sea basins, the Protozoa develop in mass after the decay of phytoplankton at the end of the spring bloom which cause an increase of the biomass of bacteria. The biomass of ciliates and colorless flagellates may reach 1 g/m^3 in the open sea in the layer of the main maximum up the thermocline, exceeding the biomass of the remaining zooplankton. Massive development of bacteria and Protozoa represents an important stage in the heterotrophic phase of the seasonal succession of the plankton community in the temperate waters. During this period, they are actively consumed by calanoids (Sorokin, 1974). The Protozoa are one of the leading components in the plankton community of the regions of upwellings (Beers, Stewart, 1971; Tumantseva, Sorokin, 1975).

As was noted above, bacteria and Protozoa represent the main nutritional component of detritus and of the bottom sediments. Direct microscopic observations (Newell, 1965; Fenchel, 1972) have shown that in the detritus which passes through the intestines of benthic animals, the population of bacteria is decreased several times due to digestion (Newell, 1965; Johannes, Satomi, 1966). Experiments with ^{14}C have proven the digestion of bacteria by amphipod sestonophages (Hargrave, 1971). Holothurians and gastropods digested the labeled microflora in the bottom sediments available to them, which provided them with a normal ration (Sorokin, 1972).

Direct correlation in the distribution of the biomass of bacteria and meiobenthos in the oceanic benthic sediment (Table 11) indicates that the bacteria represent the main nutritional component of the meiobenthos. Actually, the microflora in the sediment forms the predominant portion of the living available protein. In deep-water sediments of the oligotrophic areas of the oceans where the concentration of microflora is very low there are no benthic animals which nonselectively swallow the bottom (Sokolova, 1972).

An overall evaluation of the trophic significance of the microflora can be produced only at the level of the ecosvstem by calculating the fraction of its participation in the transformation of matter and energy of the entire community. In order to produce the corresponding information, microbiologic analyses should be conducted in combination with

Table 11. Mean values of biomass of bacteria and meiobenthos (g/m^2, wet mass) bottom sediments of various trophic zones of the Pacific Ocean (Sorokin, 1970d; Sokolova, 1972).

Type of Sediment	Bacteria	Meiobenthos
Detrital sediments of littoral zone	100 -500	20 -50
Sediments of eutrophic shelf	20 -100	10 -30
Sediments of mesotrophic slope	2 - 20	1 -10
Deep-water sediments of oligotrophic zone	0.2- 2	0.05- 1

determination of the production and biomass of the main components of the community. Work of this sort was performed during biologic voyages of the VITAYAZ' and AKADEMIK KURCHATOV (Vinogradov, 1971). An example of one of the diagrams of flows of energy in ecosystems of the pelagic zone is shown in Fig. 22. The diagram characterizes the participation of microflora in the transformation of energy in the ecosystem of the pelagic zone of the Sea of Japan in the summer (Sorokin, 1974). In the summer, after the heating of the water and formation of the thermocline, nutrients in the upper, mixed layer, 20-30 m thick, are rapidly consumed by phytoplankton, the main portion of which dies, and only a small fraction is retained, vegetating at the upper boundary of the thermocline in the layer of the primary maximum at a depth of 25-35 m. Most of the biomass of plankters consists during this period of heterotrophic bacteria and Protozoa, which represent about 2/3 of the metabolism and energy flow in the ecosystem. The energy of primary production here satisfied only 40% of the energy requirements of the heterotrophs. The remaining energy arrives from the stored energy of organic matter, created during the winter and spring bloom of the phytoplankton, which occurs during a period of low temperatures, when the metabolism of the heterotrophic forms is low. The energy of this organic matter is expended during the heterotrophic phase of the seasonal succession of the plankton community. About 70% of the respiration of all the plankton community is accounted for by bacterioplankton, about 15% by Protozoa: the ciliates, tintinnids, and colorless flagellates, which develop massively during this period in the layer of the main maximum and represent the primary food base of the copepods.

Thus, the basic trophic function of the microflora of the temperate waters consists in the transformation of the excess organic matter accumulated during the period of the bloom into microbial biomass, which, directly or via the Protozoa, as an intermediate linkage serves as an additional food source for the zooplankton during the summer period of low phytoplankton production.

In the productive region of the equatorial divergence, the bacterial population represents 70% of the metabolism of the heterotrophic portion of the community (see Table 4). The heterotrophic community is incapable of consuming and converting the mass of primary production created. The excess organic matter is carried by flows in the form of detritus and dissolved organic matter into the poorer regions of the ocean, where it is

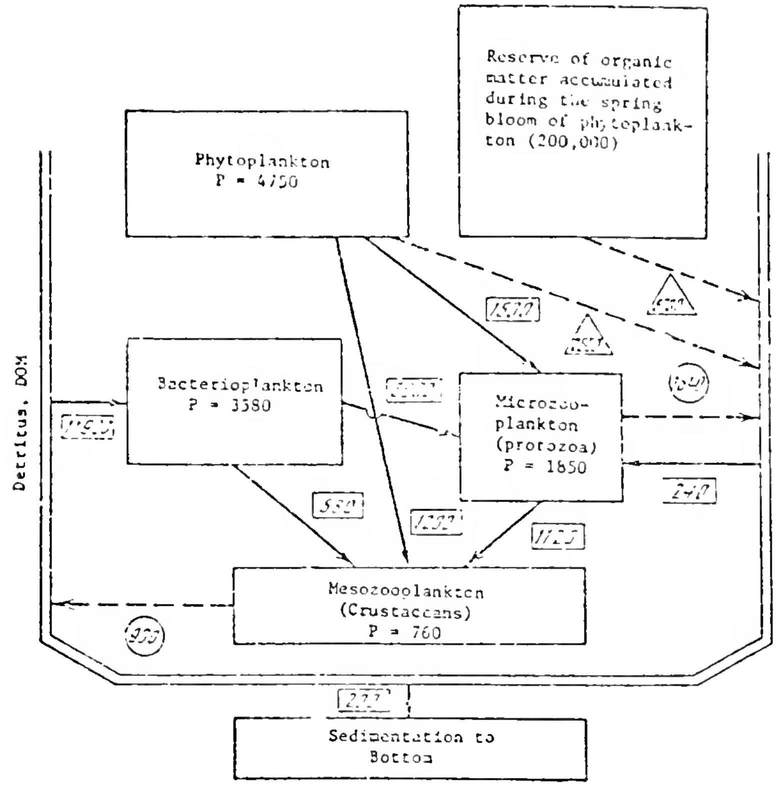


Fig. 22. Diagram of flows of energy (cal/m^2 per day) in pelagic community of central portion of Sea of Japan in the summer. Symbols same as in Fig. 12.

included in the production process by bacterioplankton and Protozoa. In the oligotrophic tropic waters and even relatively productive waters of the equatorial divergence, the primary production is insufficient to cover the energy cost of the heterotrophic portion of the community. This cost is covered by including into the metabolism, via the bacterial activity, the reserves of dissolved and suspended organic matter carried in by currents from the upwellings and subpolar convergences, where an excess of organic material is created, which is not processed by the local heterotrophic community. In the oligotrophic waters, 80-90% of the flow of energy and metabolism of the heterotrophic portion of the community is accounted for by bacteria and Protozoa, only 10-20%--by the remaining micro- and mesozooplankton. The same conclusion is reached as a result of direct measurements of the relationship of intensity of respiration of meso- and microplankton in tropical waters of the Atlantic (Pomeroy, Johannes, 1968).

To calculate the energetics of an ecosystem, the metabolism of which include external organic matter carried in from other regions of the ocean, it is very important to determine the size of this external "input". This can be done by comparing the actual production of bacteria with that which can be created by using the "internal" primary production (Sorokin, 1973d). The total energy input of the ecosystem (PP) consists of the energy of the "internal" primary production (P_p) and the energy of the external organic matter included in the production process through the bacterial link. The value of PP can be calculated if we know the primary production (P_p) and the summary production of bacteria (P_b), using the equation: $PP^p = P_b + 0.84\ P_p$. Examples of calculation are presented in Table 12. The calculations show that in tropical waters, the production of primary food may be several times more than the production of phytoplankton.

The calculations presented above demonstrate the important role of bacteria in providing a spatial energy connection between biotopes with different levels of productivity: upwellings and oligotrophic waters, subantarctic and tropical waters. In temperate waters, the microflora provide the energy connection between phases of the seasonal succession of communities. In littoral and benthic biotopes, it transforms the energy of the mass of dead organic material of the benthic sediments and detritus, dissolved organic matter, and reduced mineral products of anaerobic decomposition into living organic matter of the microbial biomass which can be assimilated. It thus forms the basic food resource, utilizing various local and external sources of energy.

Based on the information concerning the trophic structure of marine ecosystems, data on the magnitudes of rations, production of bacteria and other heterotrophic microplankton, an attempt was made to compose an approximate diagram of the flows of energy in the ecosystem of the World Ocean (Fig. 12) and, on the basis of the energy consumption of heterotrophs, to estimate the probable necessary "input" of energy into the ecosystem--primary production. Data on the production of benthos and zooplankton were taken from the works of Bogorov (1968, 1974). The biomass of microzooplankton was calculated considering data on the relationship of biomass of meso- and microzooplankton (Beers, Stewart, 1971; Tumantseva, Sorokin, 1975). The approximate production of nekton was calculated on the assumption that the total production of fish is 30 times greater than the total catch.

We find that some 80% of the energy of primary production is utilized through the detrital food chain, with the participation of bacteria and microzooplankton. This conclusion is in agreement with the data indicating a significant predominance of dead organic matter in any marine biotope. Even in the euphotic zone, the total carbon of plankton, including bacteria, is only 3-10% of the suspended organic carbon and about 0.5% of the total organic carbon in sea water (Finenko, Zaika, 1970). The direct grazing of phytoplankton by animals is about 25%, which agrees with the data on the consumption of phytoplankton in the North Atlantic (Riley, 1957). The respiration of meso- and macrozooplankton represents about 15% of the total respiration of heterotrophs, the remaining portion being accounted for by microplankton (bacteria and microzooplankton), which agrees with the results of direct determinations (Pomeroy, Johannes, 1968).

Although the ration of animals was assumed minimal, the trophic relationships in the ecosystem are found to be quite highly stressed, even if the input of primary energy is assumed to be $7.6 \cdot 10^{17}$ kcal, or about $8 \cdot 10^{10}$ t of carbon per year, which is 3.5 times greater than the primary production calculated by means of the radiocarbon method (Koblentz-Mishke et al., 1968). It is quite probable that future direct determination of this value, based on recalculated and improved radiocarbon methods will yield the same quantity: $(7\text{-}9) \cdot 10^{10}$ t C per year (Eppley, 1981).

Table 12. Biomass (B) and production of bacterioplankton and calculation of the primary food production in the tropical zone of the Pacific Ocean in waters with various levels of productivity, g C/m^2 per day (Sorokin, 1971a).

Region, depth	Depth of layer, calculated, m	Phytoplankton Production, P_p	Bacterioplankton		Primary food Production PP	$P_b:P_p$	Bacterial Destruction		$D:P_p$
			B	Production, P_b			D	D, % off stock of organic matter in water	
Butaritari Atoll Lagoon, 24 m	22	0.15	1.49	0.41	0.52	2.7	1.1	1.6	7.7
Great Barrier Reef, 70 m	70	0.62	1.20	0.81	1.27	1.3	2.3	1.6	3.7
Great Barrier Reef, 600 m	200	0.35	0.85	0.56	0.82	1.6	1.6	0.4	4.5
Great Barrier Reef, 2600 m	300	0.12	0.53	0.58	0.67	4.8	1.6	0.3	13.6
Northern Trades Current	1000	0.29	0.39	0.48	0.70	1.6	1.3	0.1	4.6
Equatorial Divergence in Western Pacific	4000	0.31	1.02	0.53	0.79	1.7	1.5	0.05	4.8
Convergence in Western Pacific	400	0.25	0.48	0.30	0.50	1.2	0.8	0.03	3.3

3. Production of Zooplankton. (E. A. Shushkina)

Determinations of the rate of production of planktonic organisms makes it possible to estimate the production of animals at various trophic levels and the plankton community as a whole, and to approach a determination of the regularities of functioning of pelagic ecosystems.

Beginning early in the 20th century, studies of the production of aquatic animals and their communities were developed throughout the prewar years (Zenkevitch, 1931; Brotskaya, Zenkevitch, 1936; Winberg, 1936; Yashnov, 1940; Juday, 1940; and others). As a result of the study of the biologic specifics of aquatic organisms of various trophic levels, approximate estimates were produced of the specific rates of their production (P/B coefficients).

In the postwar years, interest in the problem of biological productivity in aquatic environments increased still further, leading to the accumulation of extensive factual material on the production primarily of phyto- and bacterioplankton (Winberg, 1960; Strickland, 1960, 1971; Steemann Nielsen, 1960; Koblentz-Mishke et al., 1970; Sorokin, 1973e, g; and others). The studies of production of organisms of upper trophic levels (zooplankton zoobenthos, fish) developed more slowly (Zenkevitch, 1947; Greze, 1951; Elster, 1954; Shcherbakov, 1956; Kamshilov, 1958, etc.). However, since the 1960's, the problem of effective utilization of biologic resources of bodies of water became more acute, leading to a rapid increase in the number of works on estimation of the rate of production of aquatic animals, both at the populations level (Mednikov, 1960; Konstantinova, 1961; Stross et al., 1961; Greze, Baldina, 1964; Mullin, Brooks, 1970; Malovitskaya, 1971; Greze et al., 1971; Shushkina et al., 1974), and for entire trophic levels of zooplankton (Edmondson et al., 1962; Pechen', Shushkina, 1964; Zaika, 1969; Mullin, 1969, Greze, 1970; Petipa et al., 1970; V. D. Fedorov et al., 1975). These materials, produced by more precise methods than those used in the earlier years, based on a combination of experimental and field studies, allow us to approach the estimation of the intensity of the production of aquatic communities as an assemblage of organisms at various trophic levels.

In recent years, the number of studies of the production process at the community level has rapidly increased (Raymont, 1966; Petipa, 1967a; Petipa et al., 1970; Parsons et al., 1969; Winberg, 1973; Vinogradov et al., 1973). One basic method used to perform the most important task of modern hydrobiology--that of studying the regularities of functioning of aquatic communities, predicting and, in the final analysis, controlling their biologic productivity--is mathematical simulation of processes defining the function of aquatic ecosystems. This method has been ever more widely used in the past decade in the study of various problems related to the growth and production of aquatic organisms (Bekman, Menshutkin, 1964; Menshutkin, Prikhod'ko, 1968; Brocksen et al., 1970; Zaika, 1973; Shushkina, Kislyakov, 1975), the productivity of ecosystems (Menshutkin, 1967, 1971; Smith, 1972; Gupta, Houdeshell, 1973; Steele, 1974; V. I. Balyayev, et al., 1974; Winberg, Anisimov, 1969; Vinogradov et al., 1971, 1975, 1976). The significance of mathematical modelling for the solution of the problem of effective utilization of the natural resources of bodies of water is quite obvious (Krogius et al., 1969; Menshutkin, 1971; 1972; McKenzie, Mathisen, 1971).

In spite of the successes achieved in the study of the rate of production at various levels of organization of aquatic communities (species population, trophic level, community as a whole), the available data are insufficient to reveal the general regularities which define the level of production of animals in various regions of the ocean and in various geographic zones. However, in recent years some summarizing works along this line have appeared for both marine and fresh-water ecosystems (Raymont, 1966; Winberg, 1968; Mullin, 1969; Mann, 1969; Greze, 1971, 1973a, b; Zaika, 1972; Cushing, 1975; Winberg et al., 1974; Bougis, 1974; Steele, 1974).

Unfortunately, the production estimates of various authors were made by diverse methods, with various degrees of accuracy, for various seasons and periods of time, which makes any attempt to summarize the available materials and come to any definite conclusions concerning the level of production of aquatic animals in different geographic zones still more difficult. Nevertheless, it is clear (Greze, 1973a) that in the boreal regions of the ocean (Bering and Barents Seas, Northern Pacific) the annual secondary production is lower than in the southern regions (Black and Azov Seas, tropical Atlantic). The same patterns are apparently true for fresh-water ecosystems (Winberg et al., 1974; Winberg, 1975). It seems desirable to attempt to summarize the materials accumulated to date on the rate of production at various levels in pelagic communities in waters of varying trophic levels in the most studied tropical regions of the ocean and the southern seas of the USSR.

The factual material presented below was obtained primarily during expeditions conducted by the Institute of Oceanography, Academy of Sciences, USSR and, in order to avoid repetition, is only compared with results obtained and discussed in review publications of recent years (Greze, 1970, 1971, 1973a, b; Bougis, 1974; Steele, 1974; and others).

It must be emphasized that with all methods of estimation of the production rate for all trophic levels of a planktonic community, complete study of the ecosystem is necessary; it is particularly important that information be available on the concentrations of all elements of plankton in a single sample. This allows us to avoid or at least minimize the bias of estimates resulting from nonuniformity of distribution of elements of the community, unavoidable when different types of equipment are used to catch specimens at different times. In recent years, in the expeditions of the Institute of Oceanography, high capacity water bottles (100-150 ℓ) have been used, allowing us to determine the concentration of practically all plankton elements with the exception of large mobile macrozooplankton, in a single water sample (Vinogradov et al., 1976).

3.1 Methods of Calculation of the Secondary Production and Ecologic-Physiological Characteristics of Planktonic Animals

The methods of determination of the production of aquatic animals are outlined in a manuscript edited by G. G. Winberg (1968) and refined and supplemented in later works (Zaika, 1972; Greze, 1973a, b; Bougis, 1974).

Since we will be discussing basically the productivity of zooplankton in tropical regions of the ocean, where the doubling time of animals is long, it makes sense to discuss briefly the obstacles and specific features of determination of the production rate in populations which are constantly supplemented. In estimating the production of populations of this type, the most precise values are yielded by the graphic method used by G. G. Winberg and V. N. Greze, which is widely used in production studies in sea and fresh water. To determine production by this method, we must know the doubling rate of the animals, the time of development of individual age stages and the age composition of the population at known time intervals. Whereas it is rather easy to produce this information for the populations of fresh water, for marine areas, particularly open regions of the ocean with complex hydrologic conditions and significant nonuniformity of the distribution of plankton, both vertical and horizontal reliable material on the age composition of the population is exceedingly difficult to obtain, to say nothing of the difficulties involved in the study of the times of development of animals in multispecies communities. Although large numbers of publications have appeared in recent years, reporting successful cultivation and study of the time of development of individual species of zooplankton (Sazhina, 1968, 1974; Mullin, Brooks, 1970; and others), the question arises of the correctness of simple transfer of data obtained in the laboratory to natural populations. Therefore, as yet the use of the graphic method for determination of the production of populations and communities in the pelagic zone of the ocean is difficult although, for example, this method has been successfully used for the Black Sea (Greze, Baldina, 1964; Greze et al., 1968; 1971, 1973; G. N. Mironov, 1970, 1973; Petipa et al., 1970).

The physiologic method is more applicable for estimation of the rate of production in tropical planktonic communities (Winberg, 1964, 1968). To determine production by this method, we must know the number of animals N, their weight W, the mean daily metabolic rate R and coefficient of assimilated food used for growth K_2. Then, the mean daily production of the population P can be calculated from the equation

$$P = R \frac{K_2}{1 - K_2} NW \qquad (3.1)$$

Calculation of the production by graphic and physiologic methods yields similar results (Shushkina, 1972).

In estimating the production rate, all characteristics related to production, weight and metabolism are expressed in common units of measurement, preferably in units of energy--calories. This brings up the need to determine the energy equivalents of body mass and calorie content of the basic elements of the planktonic community. The energetic approach to the study of communities permits one to ignore, to a certain extent, their species composition, but in return it is very exacting in regard to information on their trophic and spatial structure.

The results of determination of the energy equivalents of body mass W_e (cal/indiv.) as a function of length ℓ (mm) for abundant planktonic animals in the tropical Pacific (Shushkina, Sokolova, 1972), which can be used for production estimates, are shown in Figure 23. Using these regressions $W_e(\ell)$ and knowing the mean length of animals of a given taxon, we can determine the mean body weight in calories W_e.

It is usually thought that planktonic animals in the higher latitudes, due to their higher content of fat, also have a higher caloric equivalent. However, comparison of the caloric equivalent of mysids in the tropical regions of the Pacific, the Black Sea and the Sea of Japan, (Fig. 24a) and chaetognaths in the same tropical regions, the North Atlantic and Sea of Japan (Fig. 24b) showed no significant difference, although it is quite probable that for other species of zooplankton, i.e., copepoda, the differences in calorie content would be greater.

The regression $W_e(\ell)$ for tropical animals of various taxonomic groups is used to calculate the mean caloric equivalent (Kcal/mg wet mass). The wet mass of animals of the groups studied was usually determined by weighing, or from the dimensions of the body, using nomograms, or empirical equations. The mean caloric equivalents thus calculated for tropical phytoplankton, zooplankton, and bacteria (Sushchenya, 1969; Troitskiy, Sorokin, 1967; Sorokin, 1971) are presented in Table 13.

Rate (R) and intensity (R/W) of metabolism of planktonic animals, usually determined on the basis of the rate of consumption of oxygen, are necessary for an estimation of the rate of production of zooplankton, the flow of energy through a planktonic community and the succession characteristics of pelagic ecosystems.

Measurement of metabolic rates in marine and fresh-water animals has been the subject of a large number of reports (reviews: Sushchenya, 1969, 1972). For marine zooplankton of various regions of the ocean, rather extensive material has been obtained by the expeditions of the Institute of Oceanology (Shushkina, Vilenkin, 1971; Shushkina, 1972; Kukina, Chistov, 1972; Shushkina, Pavlova, 1973; Pavlova, 1973; Kuz'micheva, Kukina, 1974; Klyashtorin, Kuz'micheva, 1975; Klekovskiy et al., 1975; Pasternak, 1976; Musaeva, Vitek, 1975). It has been suggested that the values of metabolic rates obtained in these experiments are significantly low due to the limited movement of the animals in the closed experimental bottle (Gruzov, 1972; Pavlova, 1973,

Table 13. Caloric equivalents (Kcal/mg wet weight) of the component plankton communities of the tropical Pacific.

Group of organisms	Dimensions,mm	K
Phytoplankton (small and large)	---	0.6
Bacteria (dispersed and aggregated)	---	1.0
Flagellata and Infusoria	---	0.8
Calanoida "broad" (length:width = 3:1)	0.5 - 10	0.75
Calanoida "narrow" (length:width = 4:1)	2 - 6	0.4
Cyclopoida (Oncaea, Corycaeus)	1 - 2	0.7
Oncaea venusta, females with eggs	1 - 3	1.0
Euchaeta marina, females with eggs	2.5 - 3.5	1.5
Euphausids	2 - 10	0.8
Ostracoda	0.8 - 3.0	0.7
Hyperiidae	2 - 3	0.7
Appendicularia	7 - 10	0.06
Salpae	7 - 10	0.01
Medusae	3 - 8	0.03
Ctenophora	2 - 10	0.03
Siphonophorae	3 - 10	0.005
Chaetognatha such as Sagitta bipunctata	3 - 10	0.9
Chaetognatha such as S. enflata	10 - 40	0.4
Pteropoda	0.6 - 5.0	0.35
Polychaeta "narrow" (length:diameter = 6-10:1)	6 - 10	0.6
Polychaeta "broad" (length:diameter = 3-4:1)	3 - 5	0.8

1974); however, studies of recent years (Kuz'micheva, Kukina, 1974; Klyashtorin, Kuz'micheva, 1975; Musaeva, Vitek, 1975) have indicated that the values of rate of oxygen consumption obtained in closed bottles, are only slightly lower and are quite suitable for approximate estimates of production using the physiologic method. As concerns the influence of feeding conditions on this parameter, individual observations have shown that the metabolic rate does not actually depend on the concentration of food (Shushkina, 1966; Shushkina, Klekovskiy, 1968; Kryuchkova, 1972).

Some results of measurement of metabolic rate R as a function of body weight W_e, cal, for planktonic animals in the tropical water of the Pacific Ocean are presented in Figure 25. A comparison of the values of metabolism for copepoda in the oligotrophic regions of the Pacific at 30°C (Shushkina, Pavlova, 1973) with metabolism measured in the regions of the equatorial upwelling at 20-22°C (Musaeva, Vitek, 1975) showed that there was no significant difference (Fig. 26). If the regression line of metabolism R to weight W at 30°C is adjusted to 20°C, using the temperature correction suggested by L. M. Shushchenya (1969), the

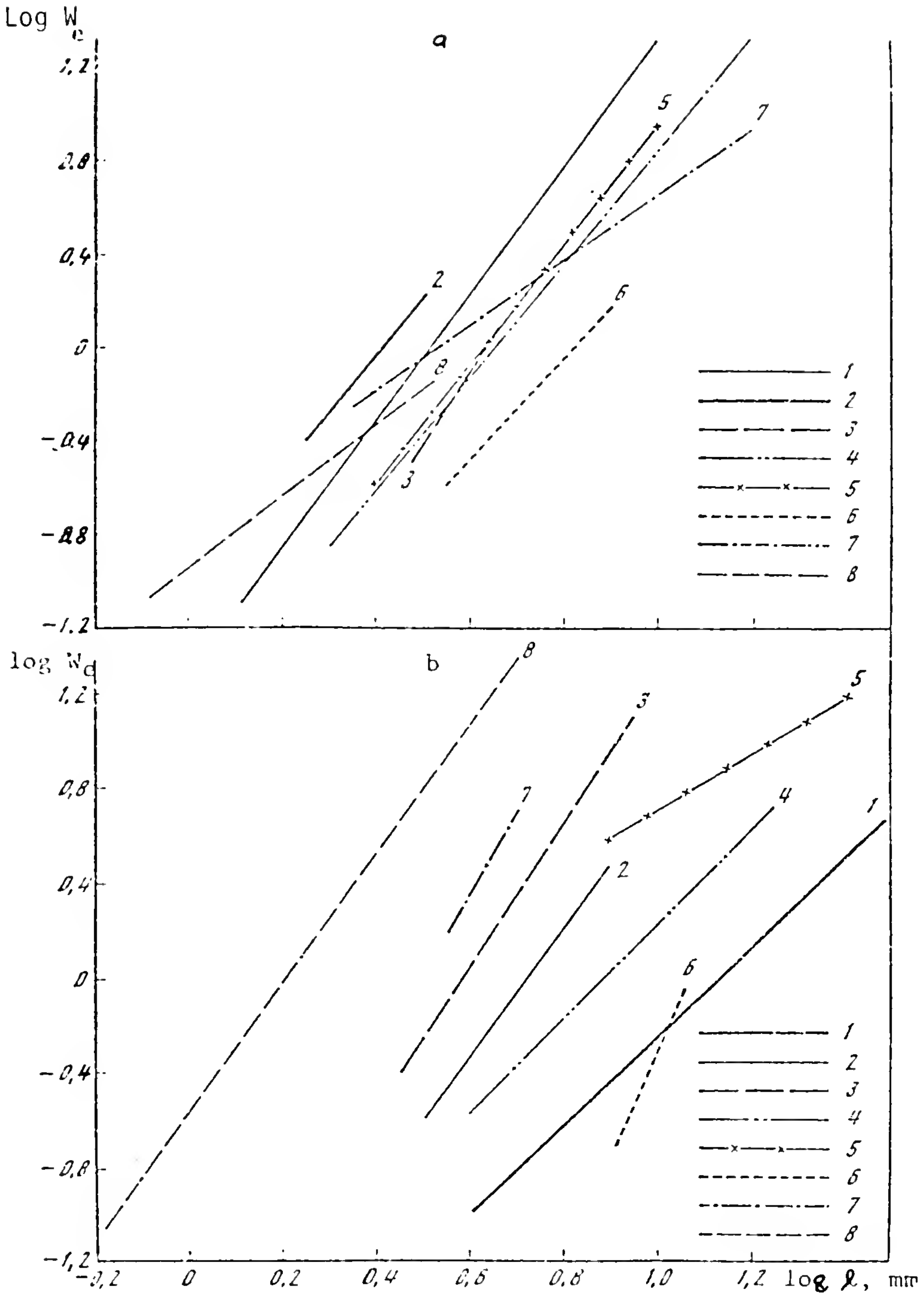


Fig. 23. Caloric equivalents of body mass W_e (cal/indiv.) of tropical planktonic animals of various lengths ℓ (mm). a - crustaceans: 1 - Calanoida, length:width = 3-3.5:1; 2 - Calanoida, length:width = 2-2.5:1; 3 - Eucalanus attenuatus; 4 - Euphausiacea; 5 - Mysidacea; 6 - Lucifer; 7 - Hyperiidea; 8 - Ostracoda; b - other; 1 - Chaetognatha; 2 - Medusae; 3 - Ctenophora; 4 - Siphonophora; 5 - Salpae; 6 - Appendicularia; 7 - Polychaeta; 8 - Pteropoda.

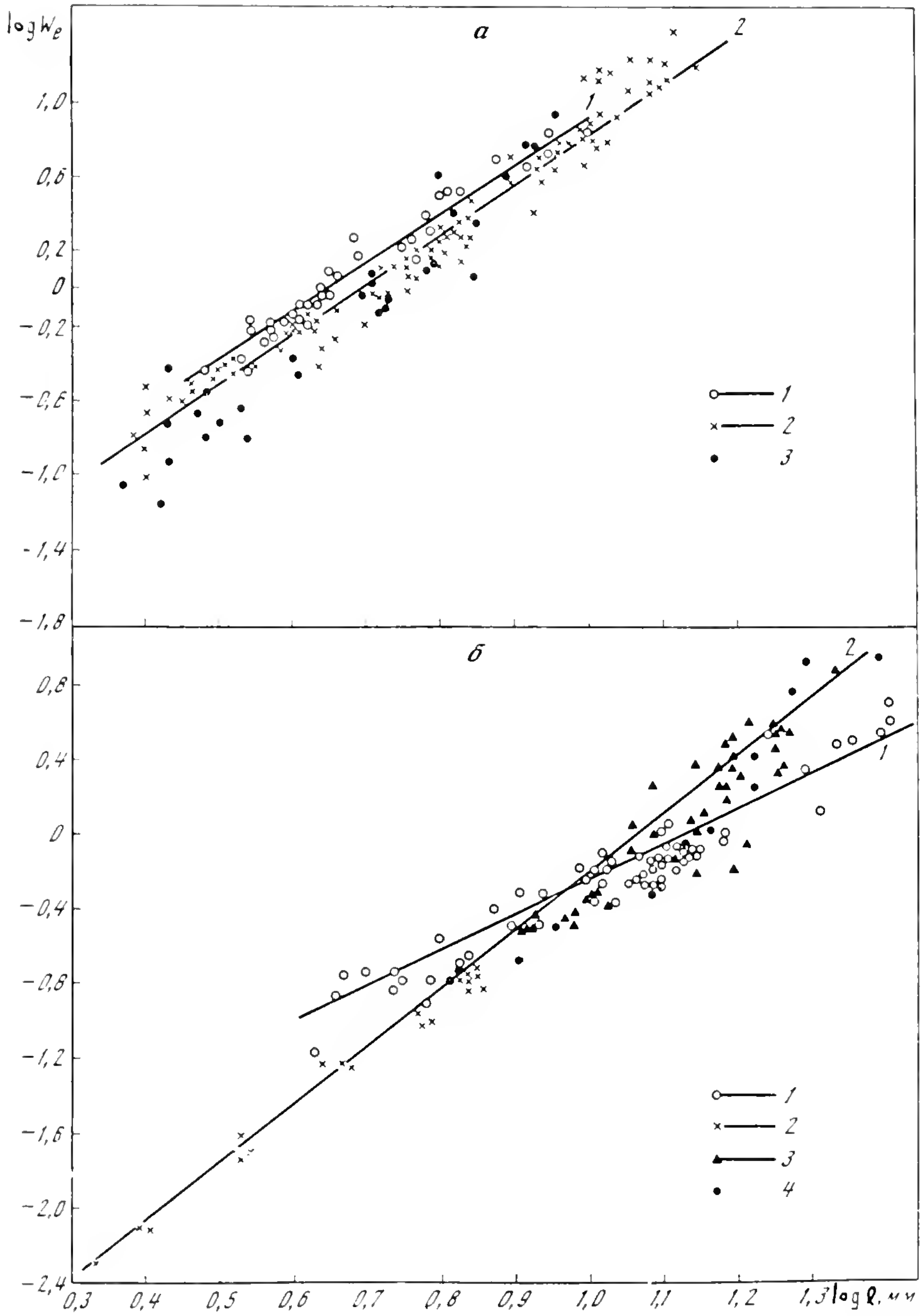


Fig. 24. Caloric equivalents of body mass W_e (cal/indiv.) as a function of size (mm) of mysids (a) and chaetognaths (b) of various latitudes. a - 1 tropical waters (reported by E. A. Shushkina and I. A. Sokolova); 2 - Sea of Japan (reported by E. A. Shushkina and V. I. Kuz'micheva); 3 - Black Sea (reported by V. N. Mikheyev); b - 1 - tropical waters (reported by E. A. Shushkina and I. A. Sokolova); 2 - Sea of Japan, littoral waters (reported by E. A. Shushkina and A. G. Timonin); 3 - Sea of Japan, open sea (reported by I. V. Kukina); 4 - Antarctic waters.

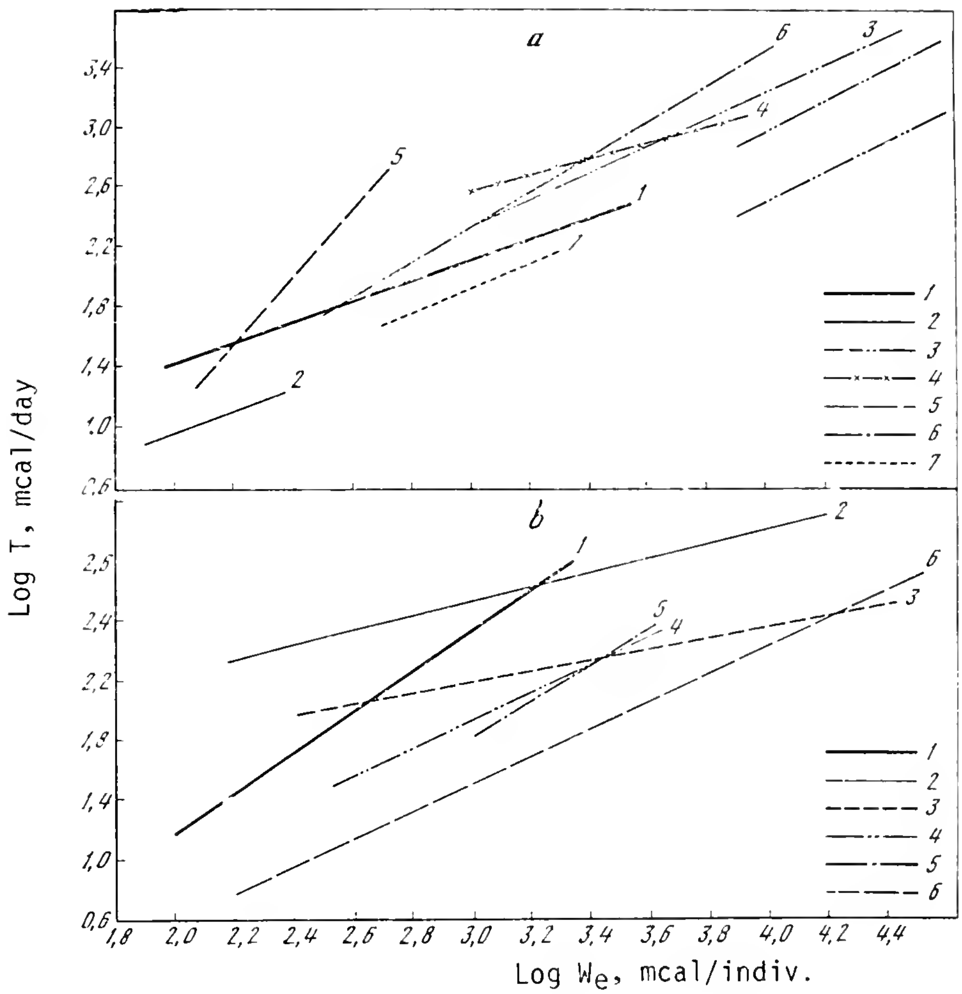


Fig. 25. Dependence of the rate of respiration R (mcal/day per individual) upon the body weight W_e (mcal/indiv.) in tropical planktonic animals. a - crustaceans: 1 - Calanoida; 2 - Cyclopoida; 3 - Euphausiacea; 4 - Mysidacea; 5 - Ostracoda; 6 - Hyperiidea; 7 - Lucifer: b - other: 1 - Chaetognatha; 2 - Medusae; 3 - Ctenophora; 4 - Siphonophora; 5 - Polychaeta; 6 - Pteropoda.

regression line presented falls significantly below the line obtained experimentally at 20°C. Thus, we can draw the preliminary conclusion that the level of metabolism of tropical copepoda at 30°C is close to the level of metabolism of crustaceans of the temperate latitudes at 20°C. This confirms once more the opinion that the metabolism of animals at different latitudes is adapted to the environmental temperature (Fox, 1936; Sholander et al., 1953; Pavlova, 1967;

Sushchenya, 1969, 1972; Shushkina, Vilenkin, 1971; Edwards, 1973). In calculating the production of tropical zooplankton in the euphotic layer from the metabolic rate, the temperature corrections apparently should not be introduced.

Calculation of the mean daily value of production by the physiologic method presumes knowledge of the mean coefficient of utilization of assimilated food for growth K_2 for the population or group of animals studied. As follows from equation (3.1), the value of K_2 is determined by the ratio of production to assimilated food, i.e., to the sum of production plus the cost of metabolism. Determination of production requires regular observation of the growth of animals, plus knowledge of the regularities and rates of their breeding. Therefore, the volumes of accumulated factual material on the values of K_2 for aquatic animals is not sufficient to allow reliable conclusions to be drawn, although a number of works have been published, dedicated to the analysis of the variability of this coefficient (Sushchenya, 1969; Shushkina, Klekovskiy, 1966; Kryuchkova, 1967, Sushchenya, 1970; Ivlewa, 1970; Mullin, Brooks, 1970; Soldatova, 1970; Shushkina, 1972; Bougis, 1974; Zaika, 1974; Pasternak, 1974; Khmeleva, 1967). The studies which have been performed indicate several conclusions concerning probable changes in maximum and average values of K_2 and the influence of environmental factors on this quantity.

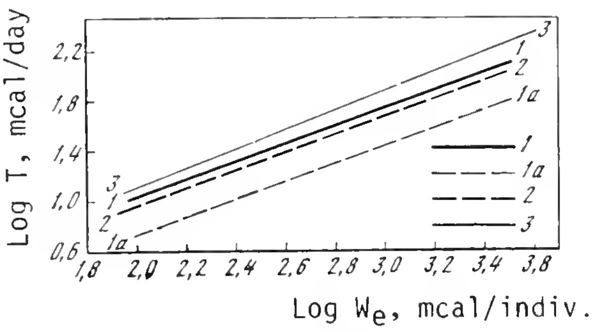


Fig. 26. Dependence of the metabolic rates R (mcal/day per individual) upon the body weight W_e (mcal/indiv.) for copepoda at various t, C. 1 - tropical Calanoida at 30°C (Shushkina, Pavlova, 1972); 1a - same, adjusted to 20°C using temperature correction suggested by L. M. sushchenya (1969); 2 - tropical Calanoida at 20°C (Musaeva, Vitek, 1975); 3 - Calanoida at 20°C (Sushchenya, 1969).

For rapidly growing species and populations under optimal conditions, the value of K_2 is near 0.6 (Winberg, 1964, 1973; Klekowski, Shushkina, 1966; Sushchenya, 1970), although during some periods of development (embryonal, older nauplial stages of copepoda, young cladocera, etc.), K_2 may be as high as 0.7-0.8 (Winberg, 1956, 1968; Zaika, 1974; Bougis, 1974). Many authors assume that for natural populations of aquatic animals, the mean value of K_2 is closer to 0.3-0.4 (Winberg, 1966; 1973; Sushchenya, 1970; Greze, 1971; Shushkina, 1972; Pasternak, 1974, Zaika, 1974).

It is probable that the value of K_2 depends directly on temperature (Ivlewa, 1970; Mullin, Brooks, 1970) and feeding conditions (Klekowski et al., 1972; Winberg, 1968; Klekovskiy, Shushkina, 1968; Mullin, Brooks, 1970) and changes irregularly with the age of the animals (Dryuchkova, 1967; Soldatova, 1970; Shushkina, 1972; Klekovskiy, Shushkina, 1977), particularly if the value of production defined considers the increase due to formation of reproductive products and exuvia (Kmeleva, 1967). On the other hand, many authors report sharp, irregular fluctuations in the values of K_2 in various stages of development of aquatic animals (Soldatova, 1970; A. F. Pasternak, 1974).

Studies have shown that in calculating the mean daily value of production of zooplankton on the basis of the physiologic method, one can take $K_2 = 0.3\text{-}0.4$ as the average value for a specific population, with 0.6 as the maximum value.

An estimate of the rate of production of individual trophic levels (specific associations) in the communities studied can be obtained by adding the production of specific populations of animals of the trophic level in question, if there is no cannibalism. In certain cases, the rate of production of phytophagous planktonic animals can be estimated by the radiocarbon method (Chmyr, 1967); however, methodologic difficulties make it necessary to correct the results produced by other methods (Shushkina, Sorokin, 1969). Individual comparison of the values of production determined by the radiocarbon and physiologic methods have yielded similar results (Shushkina, 1971; Malovitskaya, 1971).

3.2 Methods of Calculation of the Production of Communities

Production rates of communities consisting of organisms of various trophic levels cannot be determined by simple addition of the production of individual trophic levels, since this sort of addition yields a clearly elevated estimate.

Net production of the whole plankton community (P_0), which according to Winberg (1960) is equal to:

$$P_0 = P_p - \sum_{i=B}^{s} R_i \qquad (3.2)$$

where P_p is primary production, R_i is the metabolic rate of different elements of the community from bacteria (b) to predatory animals (s).

The value P_0 can also be calculated in another way (Zaika, 1972; Shushkina, 1966):

$$P_0 = \sum_{i=p}^{s} P_i + \sum_{i=B}^{s} D_i - \sum_{i=B}^{s} C_i = \sum_{i=p}^{s} P_i - \sum_{i=B}^{s} C_i \cdot U_i^{-1} \qquad (3.3)$$

where P_i is production of different elements of the community from phytoplankton (p) to carnivores (s), D_i - nonassimilated food; C_i - value of food consumption; U^{-1} - food assimilability.

Both equations (3.2 and 3.3) are practically the same.

It is possible to calculate the part of community production that may be utilized by higher trophic levels not accounted for in the calculations (carnivorous fishes, squids), or by any other form of exploitation (Shushkina, 1966; Klekowski, 1970).

It is real community production (P_r):

$$P_2 = \sum_{i=a}^{s} P_i - \sum_{i=f}^{s} C_i \qquad (3.4)$$

where P_i is production of different elements of community from protozoans (a) to predatory animals (s) and C_i is value of food consumption of the elements from herbivorous animals to predators.

The rate of production of a planktonic community can be calculated using equation (3.4) if the community includes only a small number of species, interrelated primarily by the trophic chain. Communities of this sort are relatively frequently seen in fresh and marine bodies of water in the temperate and high latitudes. However, in this case as well, the calculation of the production of zooplankton is rather difficult, since it requires us to consider the influence of such environmental factors as temperature, concentration of food for each element of the community, etc., on all of the parameters included in equation (3.4). Calculations of production for an entire tropic pelagic community, consisting of hundreds of species, interconnected in a trophic chain, are practically impossible without the use of mathematical modelling and computers.

The method of mathematical modelling in combination with radiocarbon and physiologic methods, can be used to estimate the rate of production of individual specific populations (Shushkina et al., 1974), the trophic levels of zooplankton and the planktonic community as a whole (Shushkina, Kislyakov, 1975). Such a combination of different methods was, for example, used to estimate the productivity of pelagic communities of the Sea of Japan (52nd cruise of the VITYAZ) and the equatorial zone of the Pacific Ocean (17th cruise of the AKADEMIK KURCHATOV). The essence of the approach is that at the level of maximum concentration of plankton, large (140 ℓ) water bottles of organic glass collect samples of water, including a known quantity of phytoplankton, preliminarily labeled with radiocarbon to a constant level. After 10 or 12 hours exposure of the water bottle at the same depth during the dark hours of the day, the concentration N, dimensions ℓ, weight W and radioactivity G of organisms of the phytoplankton, bacteria, protozoa and individual systematic or trophic groups of zooplankton (fine filter feeders, small herbivores, cyclopoids, predaceous calanoids, etc.) are determined. A plan is then constructed of the basic trophic connections between the elements of the community which are distinguished, nutritional selectivity coefficients are selected and the increase in weight (production) per unit of time (per day) is described for each of the elements distinguished:

$$\frac{dW_i}{dt} = C_i U_i^{-1} - R_i \qquad (3.5)$$

It is desirable to consider how the assimilation U_i^{-1} is influenced by the degree of trophicity of the waters, membership in a predaceous or peaceful level of zooplankton, as well as the variation in the daily diet C_i as a function of concentration of food (Ivlev, 1955; Jergensen, 1955; Petipa, 1967; Winberg, Anisimov, 1969; Petipa et al., 1971). The assimilation of the food $U^{-1} = (P + R)/C$, apparently depends to some extent on the trophicity of the water, i.e., on the concentration of food, and decreases with increasing food concentration (Jergensen, 1955; Klekowski et al., 1966; Petipa et al., 1971, 1974). It is thought that the minimum value of assimilation U_{min}^{-1}, with an abundance of food, is near 0.4 (Winberg et al., 1965; Klekowski, Shushkina, 1966; Klekowski, et al., 1972; Petipa et al., 1975). For carnivorous animals, the assimilation of food is usually higher than for herbivorous animals (Soldatova et al., 1969; Monakov, Sorokin, 1972; Winberg, 1973). The mean value of assimilation for herbivores can be assumed to be close to 0.6 (Conover, 1966; Sushchenya, 1975), for predators--0.7-0.8.

The rate of metabolism R_i is determined experimentally by the method of Winkler or by a polarographic method for animals of each element in the community (Shushkina, Pavlova, 1973; Muscaeva, Vitek, 1975; Klekovskiy et al., 1975). All of the ecologic-physical indices included in equation (3.5) are expressed in calories.

It is assumed that the radiocarbon label introduced with the labeled phytoplankton to the portion of the planktonic community isolated in the water bottle is distributed among the elements of the community according to equation (3.5), which allows us to determine the radioactivity of the organisms C_i/W_i individually as a function of time and use it as a control to estimate the reliability of the parameters used in the model (Shushkina et al., 1974; Shushkina, Kislyakov, 1975).

We can also use the method of mathematical modelling based on equations (3.1-3.5) and the parameters which they include, in combination with physiologic methods, to estimate the rate of production of individual trophic levels of zooplankton and calculate the net production of zooplankton and of the planktonic community as a whole (Vinogradov et al., 1976). In estimating the intensity of production of populations of aquatic animals and individual trophic groups (levels) using the balance equation (3.5), we must have some idea of the spectrum of feeding of the animals studied, their trophic connections, rates of consumption of food C and its assimilation U^{-1} as a function of the concentration of the food. These parameters are rather well known for fresh water, less well known for marine planktonic communities, particularly in the tropics. Nevertheless, the experimental and field observations allow us to produce not only a qualitative, but even a quantitative description of the trophic relationships in marine planktonic communities. Based on the available materials (Jergensen, 1955; Mullin, Brooks, 1967; Zaika, Pavlovskaya, 1970; Pavlova et al., 1971; Petipa et al., 1971, 1974, 1975; Zhukov, 1974; Sorokin, 1974f, g; Sameoto, 1974; Barna, Weiss Dale, 1974; Swale, Belcher, 1974; and others) it is possible to construct a system of primary trophic connections of the community of the Sea of Japan and the equatorial region of the Pacific Ocean (Shushkina et al., 1974) and to estimate the feeding selectivity coefficient I_{ij} (Shushkina, Kislyakov, 1975; Vinogradov et al., 1976).

The rate of consumption C_{ij} of food at the jth level (group) by organisms of the ith level (group) as a function of its concentration can be described by the following equation (Ivlev, 1955; Winberg, Anisimov, 1969; Petipa et al., 1971):

$$C_{ij} = C_{ij}^{max} (1 - e^{\xi \varkappa_{ij}^{-1}}), \qquad (3.6)$$

where ξ is a coefficient which is assumed to be close to 1.0, $\varkappa_{ij}$ is the tropho-ecologic coefficient (Menshutkin, 1971). The value of the maximum diet of the ith group consuming the jth group C_{ij}^{max} is determined on the basis of the maximum diet of species of the ith group, including all types of food C_i^{max} and the fraction which the biomass of the jth group represents in the total biomass of food, considering feeding selectivity (Shushkina, Kislyakov, 1975; Vinogradov et al., 1976). The quantity C_i^{max} can be described (Winberg, Anisimov, 1969) on the basis of the cost of metabolism R and the maximum possible increase, given that metabolism P^{max}, based on equations (3.1) and (3.5):

$$C_i^{max} = (P_i^{max} + R) \cdot U_{min} = R(\frac{K_2^{max}}{1-K_2^{max}} + 1) \cdot U_{min}. \qquad (3.7)$$

3.3 Estimate of Production of Populations, Trophic Levels, Zooplankton and the Planktonic Community as a Whole

Based on equations (3.1-3.7), we can estimate the intensity of production--the mean daily P/B coefficients--for individual populations, for trophic and systematic groups of planktonic animals, for all zooplankton, and for the planktonic community as a whole.

The estimate of mean daily P/B coefficients for various groups of marine tropical plankton, performed by a physiologic method, is presented in Table 14. The initial data for calculation, obtained in the western Pacific (44th and 50th cruises of the VITYAZ') allow us to determine the range of change of P/B coefficients with the most probable values of K_2 (0.3-0.4) within limits of dimensions of animals for which the energy equivalents ($W = bl^m$) and metabolic rate ($R = aW^1$) have been

Table 14. Calculation of mean square P/B coefficients of planktonic animals of the Pacific Ocean by the physiologic method.

Group of Animals	Body length ℓ,mm	$W = bl^m$ meal/indiv.			$R = aW^\alpha$ meal/day·indiv.			k	$P/B = \nu \cdot \ell^k$			
									$K_2 = 0.3$		$K_2 = 0.4$	
		Number of measurements	b	m	Number of measurements	b	α		v	P/B,%	v	P/B,%
Calanoida, length: width = 3.0-3.5:1	1.5- 5.5	210	43	2.6	139	1.13	0.7	-0.78	0.16	12- 4	0.25	18- 7
Calanoida, length: width = 2.0-2.5:1	1.9- 3.1	18	132	2.3	47	1.13	0.7	-0.69	0.11	7- 5	0.17	11- 8
Calanoida, length: width = 4.0:1	2.9- 4.4	20	11	3.0	66	1.13	0.7	-0.90	0.24	9- 6	0.37	14-10
Cyclopoida	1.3- 1.75	13	43	2.6	31	0.40	0.7	-0.78	0.06	5- 3	0.09	7- 5
Euphausiacea	5.0-14.0	89	27	2.3	29	0.42	0.9	-0.23	0.13	9- 7	0.20	14-11
Mysidacea	4.6- 8.9	36	24	2.5	8	13.3	0.5	-1.25	1.16	18- 7	1.81	27-11
Lucifer	5.0- 7.4	18	22	1.9	13	0.59	0.7	-0.57	0.10	4- 3	0.15	6- 5
Ostracoda	0.9- 2.5	23	116	1.5	12	0.0005	2.2	1.8	0.06	6-34	0.10	10-53
Hyperiidea	2.4-16.0	25	240	1.4	27	0.07	1.2	0.28	0.09	12-20	0.14	18-31
Chaetognatha	4.6-20.0	58	8	1.8	28	0.04	1.3	0.53	0.03	7-15	0.05	11-23
Pteropoda	0.9- 5.0	64	190	2.9	35	0.07	0.9	-0.29	0.02	2- 1	0.03	3- 1
Polychaeta	6.0-14.0	4	1140	0.4	10	0.02	1.2	0.08	0.03	4- 4	0.05	6- 7
Ctenophora	3.0- 9.1	11	17	3.0	13	15.7	0.3	-2.1	0.93	9- 1	1.45	15- 1
Siphonophora	4.3-14.0	17	18	2.0	13	0.13	0.9	-0.2	0.03	3- 2	0.05	4- 3
Medusae	3.2- 8.0	15	11	2.7	11	9.91	0.5	-1.35	1.35	27- 8	2.10	42-13

measured. The mean daily P/B coefficients for most mesoplanktonic animals have been found to be 5-15%, corresponding to the data of other authors (Greze, 1971, 1973a, b; Malovitskaya, 1971, 1973). It should be emphasized that the physiologic method using values of K_2 constant for the entire population and ignoring the specifics of the food, the pressure of predators and other factors which influence the values of production, can produce only approximate values of production and P/B coefficients. A more precise estimate of the level of production can be obtained by combining the physiologic and radiocarbon methods with mathematical modelling in experiments in situ. This type of estimate has been made for the planktonic animals of the Sea of Japan (Shushkina et al., 1974) and the equatorial region of the eastern Pacific (Shushkina, Kislyakov, 1975). The results of the determinations (Table 15) in some cases were close to the values determined by other methods, for example for the copepodites of Calanus plumchrus (Parsons et al., 1969) and the chaetognaths (G. N. Mironov, 1970, 1973; Zaika, 1969). However, most of the determinations differed significantly from the values produced earlier for closely related animals (Greze et al., 1968; Malovitskaya, 1971, 1973). Since the P/B coefficients which were compared were produced by different methods for different species of animals differing in their size and conditions of life, close similarity of the P/B coefficients should not be expected.

It is thought that the intensity of production depends on temperature conditions, since they determine the growth rate and breeding rate of animals (Mednikov, 1965; Zaika, Malovitskaya, 1967; Reeve, 1970; and others), the availability of food (Winberg et al., 1965; Shushkina, 1966; Menshutkin, 1971) and the dimensions of the animals (Zaika, 1972). This last variation--the increase in rate of production with decreasing size of the animals--is, apparently, general in nature.

The results of estimation of the intensity of production of populations and individual systematic groups of planktonic animals do not allow us to make a judgement concerning the rate and intensity of production of entire trophic levels, of zooplankton and of the plankton as a whole, which is most important in the study of the production characteristics of aquatic communities. Very few estimates of this type have been made for marine plankton (Mednikov, 1960; Petipa et al., 1970; Greze, 1970, 1971, 1973a; Vinogradova, Gruzov, 1972; Shushkina, Kislyakov, 1975; Vinogradov et al., 1976; V. D. Fedorov, 1970).

As an example, let us present the results of estimation of the productivity of various levels of the planktonic community in the upper (0-150 m) layer of water in the equatorial region of the eastern Pacific, obtained by combining the physiologic method with mathematical modelling [equations (3.1-3.5)]. The material was collected during the 17th cruise of the AKADEMIK KURCHATOV in 4 measurement areas with trophicity decreasing from east to west. The planktonic community was subdivided into: phytoplankton, bacteria, protozoa and mesoplankton. The phytoplankton was subdivided into small (cell diameter $<$ to 15 μm, volume $< 1{,}000\ \mu m^3$) and large (diameter $> 15\ \mu m$, volume $> 1{,}000\ \mu m^3$). The bacteria, which represented a single trophic level in our example,

Table 15. Mean daily intensity of production (P/B coefficients, %) for planktonic animals of various lengths ℓ (mm) and weight W (mcal/indiv.) in the Pacific Ocean and Sea of Japan.

	Pacific Ocean						Sea of Japan		
	Eutrophic Waters			Oligotrophic Waters					
Animals	ℓ	W	P/B	ℓ	W	P/B	ℓ	W	P/B
Nauplii of copepoda	0.25	1.1	96	0.18	0.5	138	0.20	1.0	27
Small copepoda (<1 mm)	0.9	10	25	0.6	3.7	50	--	--	--
Pseudocalanus (III-IV copepodites)	--	--	--	--	--	--	0.75	10.5	18
Eucalanus, copepodites	2.6	167	55	--	--	--	--	--	--
Calanus plumchrus, IV copepodites	--	--	--	--	--	--	3.1	1120	4.8
Scolecithrix	--	--	--	2.5	474	30	--	--	--
Centropages	1.8	116	36	--	--	--	--	--	--
Calanus australis, copepodites	2.0	265	27	--	--	--	--	--	--
Oithona	0.9	4.5	65	0.6	2.0	106	0.6	2.4	61
Oncaea	0.8	15	30	0.65	8.0	60	--	--	--
Microsetella	0.7	4.0	98	--	--	--	--	--	--
Euphausiacea, juveniles	4.0	450	42	3.0	782	28	--	--	--
Doliolum	1.5	4.0	97	--	--	--	--	--	--
Chaetognatha	15.0	1070	17	6.3	250	20	7.9	135	11
Polychaeta	2.2	85	42	--	--	--	--	--	--
Siphonophorae	7.6	200	43	3.4	20	75	--	--	--
Fish larvae (*Scomber*, *Myctophidae*	5.5	1400	48	--	--	--	--	--	--

included dispersed forms and aggregates (diameters > 4-5 μm). The protozoa, belonging, probably, to at least 2 trophic levels, were subdivided into small heterotrophic flagellata (diameters ≈ 3-5 μm), feeding on small phytoplankton and dispersed bacteria, and infusoria, feeding on phytoplankton, bacteria and flagellata. The mesozooplankton was subdivided into 2 trophic levels: omnivores with primarily filter-type feeding, consuming phytoplankton, bacteria and protozoa and catching predators, consuming infusoria, omnivores and animals of their own level. The omnivores included: fine filter feeders (appendicularia and doliolids), the primary food of which consisted of small phytoplankton, bacteria and flagellata; small copepoda (nauplii, copepodites of copepoda and mature calanoida measuring up to 1 mm), feeding on phytoplankton, aggregated bacteria and protozoa; nonpredaceous large calanoida (*Undinula*, *Eucalanus*, *Nannocalanus*, etc.), consuming phytoplankton, aggregated bacteria and infusoria. The mesoplanktonic carnivores were represented by: cyclopoida, the food for which consisted of the infusoria, fine filter feeders and small copepoda; predaceous calanoida (*Euchaeta*, *Candacia*, etc.), feeding on fine filter feeders, small copepoda, and cyclopoida; other carnivores (primarily chaetognatha, polychaeta and hyperiids), consuming all omnivores, cyclopoida and predaceous calanoida.

The rate of production of the lower trophic levels (phytoplankton and bacteria) decreased with decreasing trophicity of the water from 18 (phytoplankton) and 6.6 Kcal/m^2·day (bacteria) in the zone of most intensive upwelling (97°W) to 3.2 and 2.3 Kcal/m^2·day at 140°W. For the mesozooplankton, and particularly the predaceous forms, this decrease was less strongly expressed. For example, for the cyclopoida, the rate of production decreases from 0.7 to 0.1, while for all predators except copepoda, it decreases from 0.4 to 0.1 Kcal/m^2·day. The specific production (mean daily P/B coefficients) for the phytoplankton and bacteria increase as the water becomes poorer, decreasing for the protozoa and mesozooplankton.

It has been repeatedly stated that a young community, forming in the eutrophic waters of an upwelling, accumulates energy, and then, as the community develops, the water "ages" and the trophicity decreases, the energy is expended (Vinogradov et al., 1971). The data obtained in the equatorial eastern Pacific allow us to explain the mechanism of this process. As we move from east to west along the zonal component of the surface equatorial current, the trophicity of the water and biomass of all primary groups of microplankton and mesoplankton decrease, particularly that of the phytoplankton and bacterioplankton. The degree of satisfaction of the food demands decreases, the stress of trophic connections increases and the effectiveness of energy transfer through the system increases. The significance of predators increases, and cannibalism increase, both within groups of protozoa, and within groups of predaceous mesozooplankton--from 50 to 80% of the production of zooplankton and almost all of the production of protozoa are consumed by individuals at the same trophic level. As a result, the total and specific daily production of these groups and of all zooplankton take on negative values. The very expenditure of energy mentioned above actually occurs. True enough, the trophic pressure on phytoplankton and bacteria is decreased in this process, which may result in a renewed increase in production of the entire community. We found this at 155°W. Apparently, the net production of the community undergoes significant, regular fluctuations against a background of overall reduction. Probably, changes in the production of the community occur analogously as it develops in other regions of the ocean.

Thus, the materials accumulated to date give us some idea of the production of populations of marine planktonic animals, of trophic levels of zooplankton and of the planktonic community as a whole. However, as we have noted, due to the paucity of factual material, it is difficult to draw any broad conclusions concerning the intensity of production of planktonic animals and zooplankton in general in waters of different trophicities and in different geographic zones of the World Ocean. However, we can hope that the problem of efficient utilization of the resources of the World Ocean which has now arisen will lead in the next few years to rapid development of studies of the process of production in marine communities, allowing us to develop descriptions of these processes for the entire World Ocean and for its individul parts, thus approaching a solution of the problem of prediction and even control of the productivity of marine ecosystems.

4. Production of the Zoobenthos.

(A. N. Golikov, O. A. Skarlato)

Estimation of the production of the macrozoobenthos involves a number of methodologic difficulties. It is very difficult to obtain reliable information on the quantitative distribution of organisms of the benthos. On hard bottoms and in stands of underwater vegetation, determination of the quantity of organisms using the standard equipment for quantitative measurement (trawls, drags, bottom diggers) yields results which are low by tens or even hundreds of times (Barnes, 1962; Skarlato et al., 1964), while in soft bottoms the results of the use of these devices will still be low by several times. The significant error in information obtained by standard quantitative benthos-counting devices from ships in comparison to the actual picture has even led to the use of the term "bottom-digger benthos". More reliable data on the quantitative distribution of the benthos can be achieved by quantitative methods of hydrobiologic research using divers (Golikov, Scarlato, 1965; Golikov, Scarlato, 1967). This method is based on direct counting of organisms in homogeneous areas of biotopes covering areas varying from 100 m^2 down to 20 cm^2, depending on the dimensions of the organisms in question and the nature of their distribution. Organisms are counted in areas, the dimensions of which vary on a logarithmic scale (100, 10, 1, 0.1 m^2, etc.) corresponding to the logarithmic distribution of organisms in biocenoses. The selection of sectors for sampling is performed by research divers, who directly (visually) estimate the degree of homogeneity of biotopes, the boundaries of biocenoses, the abundance and variety of life. This makes the quantitative method using divers relatively reliable and accurate as a method of studying the marine benthos in the upper levels of the shelf, down to depths of 30-40 m. At greater depths, in parallel with the use of trawls and bottom diggers, it is desirable to utilize underwater photography and television.

To determine the production and bioenergetics of biocenoses, one must study the production of the specific populations in these biocenoses. Obviously, reliable determination of production is impossible without knowledge of the peculiarities of growth and duration of life of the animals of a given biocenosis. Most significant for the determination of the production properties of populations is the study of the growth rate and duration of life not of individuals, but of the majority of individuals in a population. However, reliable determination of the age of individuals is usually possible only by means of cumbersome observations in cages.

The general regularities of growth of poykilothermic aquatic animals and methods of its determination are well known (Vinberg, 1968; Vilenkin, Vilenkina, 1973; Alimov, Golikov, 1974; and others); we shall discuss only 1 method of estimating the group growth of macrobenthic animals.

Determination of the group growth of individuals can be based on analysis of the dimensional and weight structure of a specific population which, in species with intermittent (not year-round) breeding, has generative discreteness (Golikov, 1970). Since in the temperate and high latitudes, practically all species of marine animals have intermittent breeding due to the elevated stenothermicity of gametogenesis and the early stages of ontogenesis (Kinne, 1970), the method of determination of the group growth and age of individuals on the basis of generative discreteness in the structure of populations is a universal one. When this method is used, one must first consider not the frequency of occurrence of individuals of a given dimensional class, as in determination of growth on the basis of the Petersen distribution or the probability paper method, but rather the distribution of individuals by actual dimensions, i.e., the presence or absence of individuals of a given size at the moment of observation. It is methodologically important to analyze the dimensional distribution of individuals based on materials collected over a relatively short time interval, so that the change in dimensions of individuals during the process of growth will not mask the generative discreteness in the structure of the population.

It is characteristic that individual variations in the growth rate of individuals within a generation, as a rule, do not exceed the differences in dimensions of groups of individuals of successive generations. This results from the unity of the gene pool of the local population, the polygenous determination of individual variability of growth and the similarity of phenotypic shifts in the growth rate for all members of a population under the influence of identical conditions. The variability in growth rate of individuals of one generation is greater in species with an extended breeding period than in those with short spawning times. Individuals born at the beginning of a breeding period grow more rapidly, survive better and achieve greater dimensions than individuals appearing near the end of the breeding period, which are subjected to the unfavorable effects of temperature in similar phases of ontogenesis (Golikov, 1975b).

Due to the asymptotic nature of growth of the overwhelming majority of marine benthic organisms, differences in the dimensions of individuals in successive generations decrease with age. The method of estimating the growth rate and age on the basis of the dimensional and weight structure of populations is suitable for species which stop growing in the later stages of ontogenesis, which usually is not characteristic of poykilothermic marine organisms. In this case, the age of the oldest generations can be approximately determined on the basis of the nonproportional increase in number of the last cohort: the largest and oldest individuals having approximately the same dimensions. Examples of generative discreteness in the structure of local populations and determination of the growth rate and duration of life of marine invertebrates on the basis of this characteristic have been presented in a number of works (Golikov, Menshutkin, 1971; Golokov, Menshutkin, 1973; Menshutkin, Golikov, 1971; Sirenko, 1973; Tabunkov, 1973, 1974; Menshutkina, 1975; and others), and are illustrated by data on the structure of populations and growth of 2 species of gastropoda with different life durations (Figs. 27 and 28).

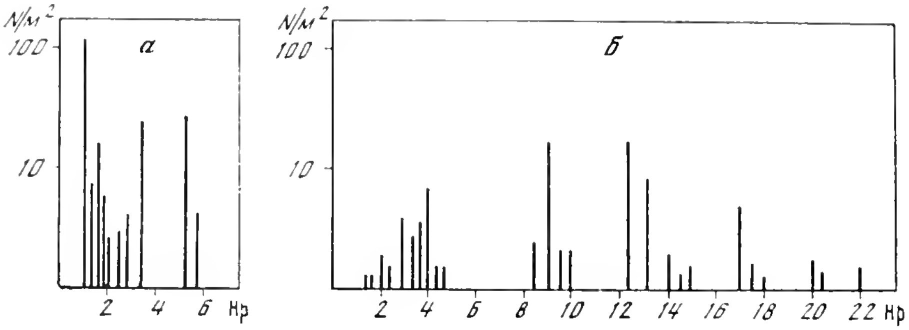


Fig. 27. Dimensional structure of populations of Minolia iridescens (a) and Littorina squalida (b) during the summer in Pos'yeta Bay, Sea of Japan. Ordinate shows number of individuals (N) per m^2; abscissa shows shell height, mm.

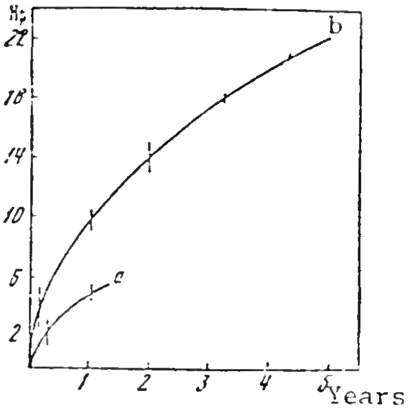


Fig. 28. Linear growth of Minolia iridescens (a) and Littorina squalida (b) in Pos'yeta Bay, Sea of Japan. Ordinate shows shell height (H_p), mm; abscissa shows age, years.

The essence of determination of growth rate and life duration of individuals in a specific population can be reduced to counting the number of corresponding generations of discrete dimensional-weight groups. In species with life cycles over 1 year in length, the first dimensional-weight group, depending on the time of sampling and the status of the population, corresponds to individuals born in the same year, or individuals at least 1 year of age, while the second belongs to individuals a year older, etc. With spawning in portions, extended metamorphosis or the formation of spring and winter subgenerations, individuals of a given year of birth form similar dimension and weight groups, corresponding to the spawning peaks, and different from each other in terms of dimensions and weight significantly less than individuals of the previous year of birth. The reliability of differences in dimensions of individuals of successive generations is usully tested by statistical methods. In an analysis of the structure of a population, it is important to have material covering most of the ecologic zones inhabited by the species in the given location. This allows us to consider individuals of different ontogenetic stages in the population, frequently restricted to different biotopes. One simple method of estimating the spatial heterogeneity of the dimensional structure of a population is to compare the frequency of occurrence of individuals of a given size in different sinusia (levels) of the biotopes and at different depths.

The relationship between dimensional and weight characteristics of individuals of a population is not difficult to estimate using the equation $W = aL^b$, where W is the weight of an individual and L is its maximum linear dimension. Studies of recent years (Alimov, Golikov, 1974; Tsvetkova, 1974; and others) have shown that the values of coefficients a and b in representatives of a single life form do not differ statistically. This greatly facilitates estimation of the parameters of the equations for various species. The weight of organisms of a single length (coefficient a) is determined by the shape of the body and the specific weight of the organisms, while the regression coefficient b is determined by the degree of allometry of growth. In calculations of production, it is desirable to use the wet mass.

In determining the production of the zoobenthos, most authors use various modifications of the Boysen-Jensen method (Boysen-Jensen, 1919), based on estimation of the total weight increase of individuals remaining in the composition of the population over the period of observation and the main weight of individuals eliminated during that time. In the simplest case, the annual production of a population is calculated by the equation: $P = B_\tau + B_e$, B_τ and $B_{\tau+1}$ are the biomass of a population at the beginning and end of the year analyzed, B_e is the biomass of individuals eliminated during the year, estimated as the difference between the initial and final populations, multiplied by the mean weight of individuals eliminated:

$$B_e = \frac{1}{2}\left(\frac{B_\tau}{N_\tau} + \frac{B_{\tau+1}}{N_{\tau+1}}\right)(N_\tau - N_{\tau+1}) \qquad (4.1)$$

This method, sometimes with slight variations, is widely used in the literature to calculate the production of massive species of zoobenthos (Boysen-Jensen, 1919; Blegvad, 1928; V. V. Kuznetsov, 1941, 1948a-c; Vorob'yev, 1949; Shorygin, 1952; Sushchenya, 1967; Masse, 1968; Khmeleva, 1973; and others). It is usually used for littoral regions, located near marine biologic institutions, since determination of production by this method requires repeated frequent sampling of materials from the same biocenoses. In the improved Boysen-Jensen method (Bekman et al., 1968; Winberg et al., 1971; and others), production is calculated by the equation:

$$P = \sum_{\tau=0}^{n} \frac{1}{2}(N_\tau + N_{\tau+1})(W_{\tau+1} - W_\tau)\frac{1}{\Delta t}\,, \qquad (4.2)$$

where N is the number of age groups, Δt is the time sector analyzed.

Considering that in a stable population (one in which upon completion of a generative cycle, the initial dimension-age structure and population are restored) of multiannual benthos organisms, the annual production (P) is equal to elimination (E), production can be estimated by the equation:

$$P = E = \sum_{\tau=0}^{n} \frac{1}{2} (W_{\tau} + W_{\tau+1}) (N_{\tau} - N_{\tau+1}) \frac{1}{\Delta t}, \qquad (4.3)$$

reflecting the mean weight of individuals eliminated from the population over the time of observation. To determine the annual production, the results of observations for individual sections of time are added.

Obviously, the accuracy of calculation of production will be higher, the more frequently observations are performed. This results from the need for the most accurate possible determination of the time of elimination of individuals in various age groups and the appearance of replacements in the new generation or by migration. If the sampling frequency is too low, the weight gain of individuals which disappeared from the population long before the moment of observation may be included in production, leading to an elevated calculated value of production or, conversely, lack of data on the time of supplementation of a population will lead to reduced values. Naturally, one must be sure that the calculation of production is performed for the same population studied at the beginning of observations.

Considering the methodologic difficulties, a number of authors have suggested that the daily growth of individuals or specific P/B coefficients of populations obtained experimentally or by mathematical calculation be used to calculate production (Konstantinov, 1967, 1970; Zaika, Malovitskaya, 1967; Greze, 1967, 1973a, b; Mathews, 1970; Zaika, 1972; Burke, Man, 1974). However, it is obvious that the P/B coefficients or cumulative daily growth of individuals in different generations depend greatly on the relationship of the populations of individuals of different ages and the conditions of existence of populations and, consequently, are essentially different during different seasons of the year and in populations living under different conditions. This once more emphasizes the need to take samples as frequently as possible in order to allow estimation of changes in population and the weight of individuals in various cohorts.

Calculation of the production of populations of benthic animals can also be performed on the basis of the ecologic-physiologic approach to estimation of the weight increase of individuals, which is dependent on the intensity of their metabolism. The production is calculated on the basis of the ratio of the growth of individuals to the cost of metabolism, which is expressed by the equation for the coefficient of net production, or the effectiveness of utilization of assimilated food for growth: $K_2 = P:(P + R)$, where P is the production (cal), R represents the cost of metabolism (Winberg, 1966, 1968; Bedman et al., 1968; McNeil, Lawton, 1970; Klekowski, 1970; Hughes, 1970; Bregman, 1971; and others). After calculating the value of K_2, it is not difficult to determine the production of individuals of various sizes (weights), then the production of the population, as the sum of the growth of all individuals present in the population during the time of the analysis. Obviously, to analyze the annual production of a population by the ecophysiologic method, it is also necessary to know the relationship of the numbers of individuals in cohorts during various seasons of the year, particularly since the rate of elimination and intensity of metabolism and growth of individuals change greatly from season to season.

As we can see, all of the methods analyzed above for calculation of production require regular, year-round observations of changes in the numbers of individuals of various ages. These observations of populations of benthic organisms are frequently impossible, particularly in areas far from scientific research institutions. Considering this fact, as well as the difficulty of tracing the dynamics of the populations of organisms in the open seas, a static-dynamic method of determination of production has been suggested, based on analysis of the size-weight and age structure of populations at the moment of observation as a result of the annual production process (Golikov, 1970). The method is based on the fact that the structure of a population is used to establish the growth rate and age of individuals (with a check on the basis of morphologic indications of growth, if there are such), after which the quantity of living matter produced by the population during the year before the time of analysis of its initial state (growth production of population P_g) is calculated by estimating the weight gain of all individuals detected at the moment of observation, using the equation:

$$P_g = \sum_{\tau=0}^{n} N_\tau (W_{\tau+1} - W_\tau) \frac{1}{\Delta t} \qquad (4.4)$$

or the classical equation (4.2).

The value of Δt in the version analyzed is equal to one year. Based on equation (4.4), the weight gain of all individuals surviving and those eliminated during the time period analyzed is calculated, while equation (4.2) is used to determine the weight gain of all individuals surviving and half of those eliminated during this period of time. Obviously, with a sharp decrease in the population of the generations at the beginning of the time sector analyzed, with relatively uniform elimination, and in those cases when the time of elimination of individuals is not known, the best result will be yielded by an estimate of the growth production using the equation generally used for this purpose (4.2). However, in those cases when most of the elimination occurs at the end of the time sector analyzed (for example, elimination after spawning), calculation of growth production by equation (4.4) may be more accurate.

Determination of growth production of a population using a single sample per year is based, as in calculation of production by the other methods analyzed above, on the idea of the relative stability of natural populations of annual species where there are stable, periodically repeating fluctuations in the environmental conditions. Actually, the supplementation of a specific population with juveniles is usually observed in a given area at a constantly defined time; for many species, at this same time, we observe the post-spawning elimination of older age groups, and the population also decreases during the winter. All of this leds to fluctuations in the numbers of various cohorts in the population which are predictable with respect to time, allowing us to assume that during different years, at the same time of year, the population has approximately the same number of individuals and total biomass, with a similar relationship of numbers of individuals of various generations. The steady nature of many natural populations and the comparability of values of growth production calculated for a given season can be shown on the example of analysis of the production process in populations of a number of species of benthic organisms in Pos'yeta Bay (Golikov, 1970; Golikov, Scarlato, 1970; Golikov, Menshutkin, 1973). A disruption of the steady nature of populations is observed upon sudden, aperiodic changes in environmental conditions, related to natural processes or human interference. Obviously, the closer the population being analyzed is to a steady state, the more precisely the calculation of its growth production can be performed, using a single sample. In a steady population, increase and elimination in all generations occurs at approximately the same time, and restoration of near-initial structure in each generation is achieved by the growth of the surviving individuals of the younger generations (supporting a portion of the production process). The very phenomenon of steadiness results from the presence of compensatory processes to replace losses in populations and elements of self-regulation in population dynamics.

The method we have presented for calculation of the annual growth production of a steady population allows us to abstract ourselves from seasonal, functional and random changes in growth rate and rate of elimination of individuals, and reflects the quantity of living matter formed during the course of the year (at the moment of observation), necessary for creation of a definite dimension-weight and age structure of the population. It allows us to determine the approximate annual growth production of the population based on a single, rather complete quantitative sample, if it is impossible to perform constant, year-round observations. The possibility of determining production on the basis of a single reliable quantitative sample of a population is also reported by G. G. Vinberg (Bekman et al., 1968, page 100). With simultaneous analysis of a population and estimation of the production on the basis of a single sample, the only significant factor is the time of disappearance of individuals from the population, since the weight growth of individuals which have moved into the subsequent age group is automatically considered. If we know the spawning time and the time of supplementation of the population with juveniles for the species of a given biogeographic complex, as well as the general regularities of elimination, we can determine the most probable periods of elimination of individuals of the population and introduce the corresponding corrections.

A model experiment to analyze the accuracy of estimation of production by this method has shown that the determination of the mean annual growth production of a population based on a single sample is rather reliable and accurate, if the time of collection of the materials is adjusted approximately to the middle of the period of supplementation of the population with juveniles (Golikov, Menshutkin, 1971). In temperate waters in the northern hemisphere, this is usually observed in the summer or early fall. This conclusion has been confirmed by analysis of seasonal changes in the production process of a number of species of gastropoda, differing in their biogeographic distribution and duration of life (Golikov, Menshutkin, 1973; Golikov, 1975b).

In cases when observation of the structure of a population is performed at a time which is not favorable for determination of the annual growth production (peak of supplementation with juveniles or maximum of elimination), the growth production calculated up to this time may differ greatly from the mean annual growth production (by up to 80%). However, 2 samples, taken at an interval of approximately 1/2 year, allows the possible error to be decreased to less than 25%, while 4 observations during the various seasons of the year allow the mean annual growth production of a population to be estimated with an error of less than 5% (Golikov, Menshutkin, 1971). If it is possible to observe the structure of a population during various seasons of the year, the mean annual growth production can be defined as the mean of the annual productions calculated for each moment of observation (P_{g_i}):

$$P_{g_m} = \frac{\sum_{i=1}^{n} P_{g_i}}{n} , \qquad (4.5)$$

where n is the number of observations.

Obviously, of greatest interest is observation of the full production of a population, including all living matter produced during the course of a year. The total production of a population must include all of the juveniles produced during a year. The total production of a population can be approximated, depending on the nature of elimination, by one of the following two equations:

$$P = N_0 W_0 + \sum_{\tau=0}^{n} \frac{1}{2} (N_\tau + N_{\tau+1}) (W_{\tau+1} - W_\tau) \frac{1}{\Delta t} \qquad (4.6)$$

or

$$P = N_0 W_0 + \sum_{\tau=0}^{n} N_\tau (W_{\tau+1} - W_\tau) \frac{1}{\Delta t} , \qquad (4.7)$$

where $N_0 W_0$ is the biomass of individuals of a given year of birth.

The production of a population includes both the weight of individuals which have disappeared from the population during the calculated time due to natural death, consumption or migration, as well as the weight gain of individuals remaining in the population at the end of the period in question. Whereas the first portion of the production process represents a sort of reserve of strength of the population, the second portion is important in principle for its very existence. To symbolize this second portion of production, which represents the quantity of living matter formed during the time of turnover of a generation (in this case--during a year) and remaining in the population, the concept of supporting production has been developed (Golikov, 1970). The supporting production P_s is responsible for the creation of that portion of the biomass of a population which is formed during the turnover of 1 generation. For species with a duration of life of individuals of more than 1 year, the supporting production is expressed as the sum of the biomass of juveniles (of the same year) and the annual weight increase of the individuals of older generations present at the beginning of the year.

$$P_s = \sum_{\tau=0}^{n} N_\tau (W_\tau - W_{\tau-1}) \frac{1}{\Delta t} , \qquad (4.8)$$

where W_τ and $W_{\tau-1}$ are the weight increase of individuals of the generation in question, which survive and remain in the composition of the population over the time interval analyzed (in this version--1 year). This same equation, with the corresponding time correction Δt, is apparently suitable for estimation of the supporting production of populations of species with durations of life of individuals of less than 1 year.

It is significant that the production process during the course of the time analyzed occurs in all generations of the population simultaneously, which allows us to generate an integral expression for the full growth production of the population and its supporting component during the same time interval. The supporting portion of production during the year preceding the time of observation, given reliable data on the quantitative structure of the population and growth of individuals, can be determined rather accurately using a single sample, regardless of the degree of steadiness of the population, since it reflects the weight increase of the surviving individuals of each generation only.

If it is possible to perform several observations, the mean annual supporting production can be determined using an equation analogous to equation (4.5)

$$P_{s_m} = \frac{\sum_{i=1}^{n} P_{s_i}}{n} . \qquad (4.9)$$

The supporting portion of the production process, not including the living matter which has disappeared from the composition of the population during the period of the change in generations, can be looked upon as a characteristic reflecting the absolute weight increase of individuals surviving through the year. The rate of growth and natural duration of life of individuals are genetically determined and vary, depending on the environmental conditions, only within limits permitted by the genotype. From this standpoint, P_s is a genetically determined characteristic of the population, resulting from the possibility of its existence under the conditions in question with a mean duration of life determined by the specific genotype and a fraction of individuals surviving through the year determined by the population curve of mortality and, obviously, showing selective preference. Correspondingly, the value of P_s is the minimum of living matter which can be formed during the course of a year, necessary for stable existence of a population of a given age structure.

Naturally, the value of P_s is always less than the biomass of the population, while the rate of turnover of matter (P_s/B coefficient) is related by a rigid, almost linear, inverse dependence to the age of the individuals which predominate in terms of number, and is approximately inversely proportional to the limiting duration of life of individuals of the given population. In populations in which the age of most individuals is $\leqslant 1$ year, the full cycle of living matter occurs in approximately 1 year and $P_s/B \approx 1$. As the duration of life increases, the value of the P_s/B coefficient decreases proportionally. In species which form several generations during the course of a year, the supporting production must be correspondly greater than the biomass. Since the mean age of individuals of a given population is determined essentially by genotypic peculiarities of the species and changes slightly during different seasons of the year, the value of the annual P_s/B coefficient, calculated for different seasons, fluctuates insignificantly. Therefore, calculation of the mean annual value of this coefficient on the basis of a single sample is rather reliable, regardless of the time it was produced.

The rate of turnover of growth production of a population (P_g/B coefficient) depends strongly on the relationship of elimination in various generations and their relative numbers and changes significantly (sometimes by several times) from season to seaon. The relationship between the growth production of a population and its supporting part depends on the age structure of the population. The greater the relative share of juveniles and individuals of the younger age groups in the population, the greater the $P_g:P_s$ ratio and the greater the prospects for the positive development of the population under these conditions. Actually, young individuals with low biomass have great potential for weight gain, and with a given level of elimination, an increase in their number creates a reserve of reliability for continued existence of the population.

If the total level of elimination is reduced, particularly in the early, most sensitive phases of postlarval ontogenesis, and the survival rate of individuals is increased (for example, by mariculture), an increase in growth production should occur, and as time passes, a proportional increase in the number of surviving juveniles should result in an increase in the biomass of the older age groups. The principle of maximum increase in the population and survival rate of juveniles and methods of its realization have been suggested for the conduct of mariculture of a number of species of mollusks in waters of the Soviet Union (Golikov, Scarlato, 1970).

In a steady population with a regular decrease in the number of individuls as they grow, growth production of each generation is always greater than the supporting production, due to the predominance of the numbers of individuals in the younger age groups. If the steady-state condition is disrupted in the direction of increasing the population of the younger age groups, positive development of the population occurs until the relationships between population and biomass of the various generations achieve equilibrium at the new level and the relationship between P_g and P_s is restored. Conversely, with a significant decrease in the supplementation of juveniles, an increase is observed in the share of supporting production, which may indicate that degradation of the population is beginning. In those cases when supplementation of the population is severely limited, supporting production may become equal to growth production or even exceed it. In this case, one can expect severe and extended depression or even disappearance of the population. Actually, when supplementation of a population is reduced, after a certain period of time has elapsed, a decrease occurs in the number of producers, which, with a fixed level of elimination, causes a still greater decrease in supplementation. A similar effect can be observed in the case of a direct and sharp decrease in the population of sexually mature individuals, leading to a significant decrease in the effectiveness of spawning, for example, due to excessive fishing of producer or sudden or unfavorable changes in the environment, usually occurring along the edges of areas of distribution. A decrease in the relative fraction of juveniles in the composition of these edge populations of a species may frequently result from a sudden decrease in the duration of temperatures favorable for breeding (Hutchins, 1947; Golikov, Scarlato, 1973), which may even lead to total absence of spawning in particularly unfavorable years. One result of this is a decrease, at first in abiotic (Kinne, 1963), then in biotic potential of the edge populations and a decrease in their growth production to the level of the supporting production, or even below it.

At the boundaries of populations, the supporting production apparently usully exceeds the growth production, which is one of the mechanisms of limiting the area of distribution of a population. For example, this phenomenon was demonstrated for a population of the bivalve mollusks Nuculana pernula in Terpeniye Bay in the Sea of Okhotsk (Tabunkov, 1974). Extensive information on the dynamics of the population indicates that, given significant changes in the structure of a population, the inertia of its development is very high and may require many years for stabilization, or may result in cyclical changes.

The fact that the supporting portion of production is calculated regardles of whether the population is steady or not allows us to assume that the P_g/P_s ratio can serve as an indicator of instability of a population and of the direction of its development (positive or degrading), with a given nature of elimination. Determination of the growth and supporting components of the production process allows us to produce a quantitative estimate of the disruption of the stability of the population which has already occurred, since a disproportion in the population of various generations may result from variations in their supplementation by juveniles and differences in the rate of elimination. Analysis of the relationships between P_g, P_s and the biomass of the population can be of significant interest for determination of the possible stable catch. Obviously, the catch in any case must be less than the supporting portion of the production process.

To illustrate the static-dynamic principle of calculation of production on the basis of a single sample of a natural population, let us present an example of simple determination of P_g (from the calculation of the gradual elimination of individuals in successive generations at the end of the analyzed time sector) and P_s, using equation (4.8) (Table 16).

The structure of the local population of Buccinum cyaneium var. tenebrosum, used as our example, from a region in the shallow eastern portion of the Barents Sea by the south island of Novoy Zemli, a region favorable for this form, reflects the status of the population in early fall. Analysis of the dimension-weight structure of the population, in combination with a study of the morphologic characteristics of growth, form the basis of determination of the rate of linear and weight growth and the duration of life of individuals of the species under these conditions (Figs. 29 and 30). Calculation of the growth production (P_g) and its supporting portion (P_s) for the population in question showed that the value of P_g was 62.5, of P_s--46.5 g/m^2 per year with a biomass of 130.6 g/m^2. Calculation of the production by this method can be reduced (with some decrease in accuracy) by averaging the weight gain of individuals of each generation over the year. As we can see from Table 16, the population in question is not stable (with a single level of elimination, supplementation of the population with juveniles differs from year to year), but is in a satisfactory condition, and, judging from the ratio P_g/P_s = 1.34/1, has a sufficient reserve to support continued existence.

The static-dynamic method was used to study the production properties of a number of species of benthic invertebrates in many regions (Golikov, 1970; Golikov, Scarlato, 1970; Golikov, Menshutkin, 1971, 1973; Sirenko, 1973; Tabunkov, 1973, 1974; Tsvetkova, 1974b; Menshutkina, 1975; Yegorova, 1975). The results of these studies allow us to analyze certain regularities in changes in the production process of populations of a single species and biogeographically different species in different sections in a body of water and in different landscape-geographic zones. Species with similar characteristics of dimensions and weight, in portions of a water area favorable for them, have similar growth rate and life duration indices for individuals, and frequently often comparable values of settlement density, rate of elimination and production of each species. Naturally, the greatest similarity with respect to these indicators is manifested by similar

Table 16. Calculation of annual production P_g and P_s of a population of *Buccinum cyaneum* var. *tenebrosum* from the eastern portion of the Barents Sea by a static-dynamic method based on one-time analysis of the status of the population in early fall.

Age, Years	Shell Height H, mm	Weight of Individuals W, g	Population N, indiv./m^2	Biomass, NW, g/m^2	ΔW_s	$N\Delta W_s$	ΔW_g	$N\Delta W_g$
0	8	0.4	1	0.4	0.4	0.4	1.1	1.1
	9	0.45	1	0.45	0.45	0.45	1.2	1.2
	10	0.5	2	1	0.5	1	1.3	2.6
	11	0.55	1	0.55	0.55	0.55	1.4	1.4
1	18	0.8	2	1.6	0.8	1.6	2.2	4.4
	19	0.85	1	0.85	0.85	0.85	2.3	2.3
	20	0.9	1	0.9	0.9	0.9	2.6	2.6
	21	0.95	1	0.95	0.95	0.95	2.85	2.95
	22	1	1	1	0.9	0.9	3	3
	23	1.3	1	1.3	1	1	3	3
	24	1.5	1	1.5	1.1	1	3	3
2	30	3.5	1	3.5	2.6	2.6	2.1	2.1
	30.5	3.8	1	3.8	2.8	2.8	2.1	2.1
	31	4	1	4	3	3	2.2	2.2
3	35.5	5.6	1	5.6	2.7	2.7	2.9	2.9
	37.5	6.7	1	6.7	2.6	2.6	3.3	3.3
4	40.5	8.5	1	8.5	2.7	2.7	4.5	4.5
	41	9	1	9	2.9	2.9	5	5
	42	10	1	10	3	3	4.5	4.5
5	46	14	1	14	4.5	4.5	3	3
	49	17	1	17	3.5	3.5	3	3
6	50	18	1	18	3.5	3.5	2	2
7	52	20	1	20	3	3	---	---
Total	---	---	25	130.6	---	46.5	---	62.5

NOTE: $\sum_{i=0}^{7}$ NW is the biomass of population B; ΔW_s is the weight gain of an individual of a given size during the current year (up to the moment of observation); for individuals born that year, it is equal to their weight, for individuals which were older, it is equal to the difference between their weight and the weight of individuals one year younger, calculated from the weight growth curve; $N\Delta W_s$ is the production of individuals present (not eliminated) of the given size in the year, adding up to the supporting production of the population P_s for the year up to the moment of observation; ΔW_g is the expected annual weight increase of individuals of a given size; for all individuals except those having the maximum size in the population, it is calculated from the curve of weight growth as the difference between the weight of individuals of a given size and the individuals a year older; $N\Delta W_g$ is the production of individuals present and eliminated of a given size over the course of the year, while in some it represents the growth production of the population P_g over the year in question up to the moment of observation.

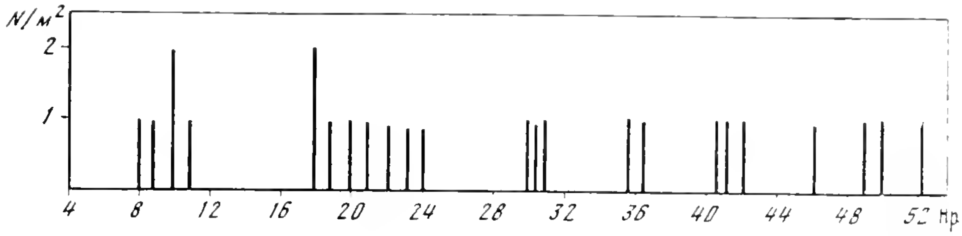


Fig. 29. Dimensional structure of a population of Buccinum cyaneum var. tenebrosum in early fall in the eastern portion of the Barents Sea. Ordinate shows number of individuals N per m^2; abscissa shows shell height H_p, mm.

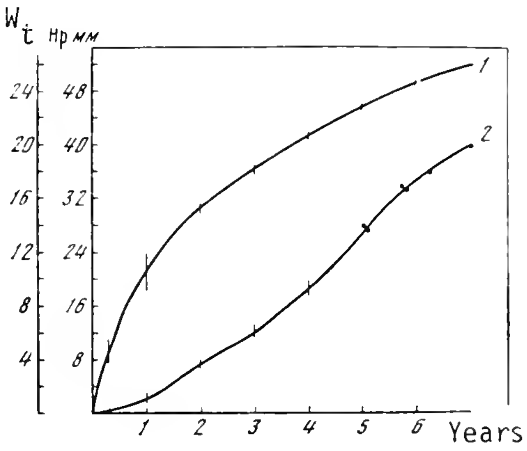


Fig. 30. Linear (1) and weight (2) growth of Buccinum cyaneum var. tenebrosum in the eastern Barents Sea. Ordinate shows weight (W_t), g and shell height H_p, mm; abscissa shows age, years.

species and genera with similar dimensions and body weights, resulting from the similarity of their metabolic activity. The fluctuations in population, biomass and production of populations are maximal for small organisms with short life cycles and comparatively greater for species with large dimensions and longer life durations. With severe, and particularly with aperiodic changes in environmental conditions due to the unevenness of the rate of elimination of species even of a single life form, the fluctuations in the production process are significantly greater than under relatively stable conditions.

The rate of the production process is related to the genetically determined thermopathy of the species. In species of warm-water origin in the northern hemisphere, the maximum production is observed in the southern portion of their areas of distribution in shallow waters and becomes quite great during the heat of summer. The mean annual value of production of these species in boreal waters can be calculated on the basis of observations made in early fall. The widespread boreal species in the southern portions of their areas of distribution yield the maximum production in spring, and reach the mean annual values of their production in early summer; in the central and northern portions of their areas of distribution the maximum production is shifted to the heat of summer, approaching the mean annual values in early fall. In Arctic waters, boreal-arctic species yield the maximum production at the end of hydrologic summer. Some high Arctic and Antarctic species show their maximum production in winter.

In water areas differing in their physical and chemical modes, the production process in populations of the same species occurs differently. Its rate increases with an increase in temperature (within the limits of the optimum for each species), while the degree of fluctuation increases with an increase in the variability of natural conditions. Thus, in the inlets of Pos'yeta Bay, a number of relatively warm-water low-boreal species reach their maximum production in midsummer, while in open areas of the bay, the maximum is reached only in the fall (Golikov, Menshutkin, 1973). Species which are subtropical in origin achieve high production in the boreal waters of the Pacific only in shallow inlets which are thoroughly heated in the summer (even if they are quite remote from each other), and are encountered only as individuals or are completely absent in nearby open, colder sections.

It is clear that in order to understand the biologic processes occurring in marine ecosystems, we must do more than study the production capabilities of populations of leading species, or even of entire biocenoses. In order to study the regularities of the cycle of biologic energy in ecosystems of various types, we must know, as a minimum, the consumption of food (C) and its assimilation (1/U) for the various trophic levels, the cost of metabolism (R), the effectiveness of utilization of consumed and assimilated food for growth (K_1, K_2) and the flow of energy through the population, or the assimilated energy ($A = P + R$). In the literature, a tremendous quantity of information has been accumulated on these parameters for marine benthic organisms. Data are also available on the calorie content of various groups of marine invertebrates and algae in sufficient quantities for measurement of the biologic processes in identical bioenergetic units--calories. Most of the coefficients necessary for calculation vary within relatively narrow ranges. Thus, for most of the organisms studied, the assimilation of food is usually 60-80% of the diet, the regression factor in the equation of metabolism as a function of weight ($R = aW^b$) averages 0.75-0.80 (Hemmingsen, 1952; Vinberg, 1966). The coefficient of effectiveness of utilization of assimilated food for growth is approximately the same for species with similar dimension-weight and age structures in a given landscape-geographic zone, averaging 0.3-0.4 for populations of macrobenthos in temperate waters. In species in the higher latitudes, this coefficient increases significantly due to the greater quantity of lipids in the food, with their high energy capacity (Golikov, 1975a, b). Of particular interest for an understanding of the trophodynamic relationships in benthic biocenoses is the study of the ecologic effectiveness of populations. This characteristic is calculated as the ratio of production of a population at the ith trophic level to the production of populations of the i-1-th level, consumed by them and, as Lindeman has shown, this characteristic averages about 10%. Preliminary calculations of the transformation of energy in the benthic biocenoses we have studied yield results which do not differ greatly from this quantity.

In connection with the above, it is obvious that the greatest difficulty in the study of the transformation of biologic energy in marine ecosystems is represented by empirical determination of the growth of individuals and the production of specific populations under their conditions of existence. However, due to the similar reaction to changing environmental factors of different specific genotypes formed under identical conditions (Golikov, 1973, 1975b), the production and bioenergetic potential of species with comparable dimension-weight characteristics under analogous conditions change in parallel. This makes modelling of the production process of populations in natural ecosystems possible, if we know the conditions of origin, density of population and weight characteristics of the species making up the populations.

CHAPTER V. MATHEMATICAL MODELLING OF THE FUNCTIONING OF A PELAGIC ECOSYSTEM

Analysis of the environment and its population as a single, interconnected system has been one of the most fruitful ideas of modern ecology, opening broad doors for the systems approach to the study of biologic processes in the biosphere. From this standpoint, the ocean and its population can also be looked upon as a single, dynamic system (Lebedev et al., 1974).

The systems approach has allowed the ideas, methods and apparatus of such mathematical disciplines as cybernetics, information theory, game theory and decision theory to be applied to the study of biologic phenomena. However, in order to actualize the capabilities of these disciplines, information on the structure and functioning of biologic objects, communities in the present case, must be summarized and formalized, and used as the basis for the construction of a model. This requires that only the basic, definitive, parameters and connections of the system be used, ignoring many interesting details. Unavoidably, this leads to some internal protest among researchers who have spent a great deal of time and effort in the study of details.

Depending on the nature of the task at hand, the degree of development and specifics of the mathematical apparatus used for its performance and the completeness of the information available on the object of study, various models can be used: for example, description of processes by differential equations (deterministic models), analysis of random processes (stochastic models) or the development of algorithms of self organization (self-organizing models). However, in any case, a model should describe the complete set of elements present in the system and their interactions, and should allow evaluation of certain situations arising in the actual systems which either cannot be directly measured or can be measured only with great difficulty.

Obviously, so-called "simulation models," allowing the use of computerized numerical models to draw conclusions concerning the behavior of a system as its various parameters change, and even allowing decisions to be made concerning the most effective methods for more traditional study of the system (Menshutkin, 1972), are of particular prognostic value. Furthermore, the construction of such models is an important means for testing the agreement of individual experimentally-observed facts. Simulation models are closely related to imitation models, differing in that they do not include a portrait description of the object due to the insufficiency of initial data on the object. These models can describe both the functioning of biologic systems and their structural peculiarities, for example the regularities of formation of horizontal (Wroblewski et al., 971; Wroblewski, O'Brien,

1976) or vertical nonuniformities in the distribution of plankton (Vinogradov et al., 1972; and others).

Another, basically different, type of model is the analytic model, used for qualitative analysis of the general characteristics of ecosystems related to estimates of their variety, stability, etc.

In what follows, we shall analyze several approaches to the modelling of marine ecosystems and their components.

1. Simulations of the Functioning of a Pelagic Ecosystem.

(M. E. Vinogradov, V. V. Menshutkin)

The functioning of marine communities is determined by a complex set of relationships between populations, based on evolutionary adaptation of organisms to existence under the conditions of the system in question. The morphophysiologic peculiarities of the organisms, their genetic characteristics, behavioral reactions, etc., play a definite role in this process. Various types of connections arise between the components of communities, but it can be considered that the basic connections in communities, integrating them and defining the basis of their structure and productivity, are food connections (Elton, 1946; Vinogradov, 1970b; and others). Therefore, the study of trophic relationships within a community, estimates of the flows of energy through the biologic system and its utilization by the various trophic groups, yield the most essential information concerning the functioning of communities.

For aquatic, and particularly pelagic, communities, the energy principle of investigation is especially effective. The significant homogeneity of the biotope determines the leading role of trophic connections in the regulation of the development of the aquatic ecosystem as a unit whole. Connections which are not directly related to feeding play a distinctly secondary role in oceanic pelagic ecosystems, in contrast to marine benthic and, particularly, terrestrial ecosystems. From this standpoint, pelagic ecosystems are the simplest for modelling and at the present time, probably, it is only for these systems that we can attempt to construct a sufficiently complete model of the balance relationships. Furthermore, the abiotic conditions, which directly effect the functioning of the community, can be quantitatively estimated with ease for the pelagic zone.

The study of the energy characteristics of the population of the deeper levels, requiring experimental observation, as yet encounters significant methodologic difficulties; therefore, we must limit ourselves to analysis of the communities of the surface (productive) zone. These communities include practically all of the phytoplankton and about half of the zooplankton of the waters of the ocean and, in fact, determine the productivity of the ocean. The study of their functioning is of singular theoretical and practical interest.

1.1 Statement of the Task of Modelling of Balance Relationships in Oceanic Pelagic Ecosystems

The construction and investigation of mathematical models of the functioning of pelagic ecosystems has a rather long history (Patten, 1968). The following works are probably among the most interesting: Riley et al. (1949), Steele (1962, 1974), Vollenweider (1965), Dugdale

(1967), and Cushing (1959a, 1969). In the Soviet Union, the works of G. G. Vinberg and S. A. Anisimov (1966) and of A. A. Lyapunov (1971), have been significant in the development of mathematical modelling of aquatic ecosystems.

The approach of A. A. Lyapunov to the modelling of complicated systems (Lyapunov, Yablenskiy, 1963) is similar in its general features to the macroscopic method of H. T. Odum (1971). The system is presented as an assemblage of relatively independently functioning elements. These elements are interconnected by various communication channels. The role of signals passing through these channels may be placed by portions of matter (energy) or information. Correspondingly, we can distinguish material and information connections between elements of the system.

One of the basic principles involved in the construction of simulations of the functioning of ecologic systems is the principle of conservation of matter and energy, which is interpreted in the form of balance relationships for each (animate or inanimate) element of the ecosystem. The mathematical model of balance relationships in an ecologic system can be constructed only if a certain degree of completeness has been reached in the study of the object being modelled. In other words, we must have an idea of the distribution of matter and energy among the corresponding elements, the regularities which define the intensity of flows among the elements, what is included in the ecosystem and what leaves or is removed from the ecosystem, and in what quantities.

A. A. Lyapunov, in composing his model, assumed that all processes occur without delay. This assumption, generally speaking, is not always correct; however, upon transition to a discrete time step, one day or more in length, the assumption of non-inertial elementary processes, for example as concerns phytoplankton, is quite justified.

The model of A. A. Lyapunov contained merely six elements: light (I), the concentration of nitrogen in assimilable ionic form (n_N), the concentration of assimilable phosphorus (n_p), the biomass of phytoplankton (p), the biomass of zooplankton (f) and the concentration of detritus (d). The following assumptions were made concerning each of these elements: light is absorbed by the water (a), phytoplankton (a_1), zooplankton (a_2) and detritus (a_3). Nitrogen and phosphorus are expended in the formation of primary production, in the process of photosynthesis (coefficients h_N and h_p) and liberated as a result of decomposition of detritus (ν_N and ν_p). The intensity of photosynthesis is limited by the light conditions and the concentration of nutrients.

$$P_p = \min(II, g_N n_N, g_p n_p), \qquad (1.1)$$

where ℓ, g_N and g_p are coefficients.

The consumption of phytoplankton by zooplankton is assumed to follow Volterra (coefficient β). The effects of multiplication of zooplankton, consumption of detritus by zooplankton and the process of cannibalism are considered analogously (coefficients γ_1, γ_2 and γ_3). The natural mortality of the zooplankton (ε) and rate of vertical migrations (ω_2) are also considered.

It is assumed that detritus is formed from dying zooplankton, and also from zooplankton excreta, the quantity of which is proportional to the quantity of food consumed (coefficients δ_1, δ_2, δ_3). The phytoplankton does not die, but is completely consumed by the zooplankton. The decomposition (μ) and settling (ω_3) of the detritus are considered. The dissolved compounds of nutrients, phytoplankton, zooplankton and detritus are carried in the vertical direction by turbulent diffusion, the intensity of which is described by coefficient K. The depth axis z is assumed to be directed from the surface of the water downward.

The systems of equations of the model are therefore:

$$\frac{\partial I}{\partial z} = - I \ (a + a_1 p + a_2 f + a_3 d). \qquad (1.2)$$

$$\frac{\partial n_N}{\partial t} = - h_{NPpP} + N_N d + \frac{\partial}{\partial z} (K \frac{\partial n_N}{\partial z}). \qquad (1.3)$$

$$\frac{\partial n_p}{\partial t} = - h_{pPpP} + N_p d + \frac{\partial}{\partial z} (K \frac{\partial n_p}{\partial z}). \qquad (1.4)$$

$$\frac{\partial p}{\partial t} = d_{PpP} - \beta pf + \frac{\partial}{\partial z} (K \frac{\partial p}{\partial z}) + \frac{\partial}{\partial z} (\omega_1 p). \qquad (1.5)$$

$$\frac{\partial f}{\partial t} = \gamma_1 pf - \gamma_2 f^2 + \gamma_3 fd - \varepsilon f + \frac{\partial}{\partial z} (K \frac{\partial f}{\partial z}) - \frac{\partial}{\partial z} (\omega_2 f). \qquad (1.6)$$

$$\frac{\partial d}{\partial t} = \varepsilon f - \mu d + \delta_1 pf + \delta_2 f^2 + \frac{\partial}{\partial z} (K \frac{\partial d}{\partial z}) - \frac{\partial}{\partial z} (\omega_3 d). \qquad (1.7)$$

Figure 1 presents a schematic diagram of one cell of the model. The symbols used in the figure will be retained throughout this entire section and serve as a language for the description of the structure of the model of an aquatic ecologic system.

1.2 Model Simulating the Vertical Distribution of Elements of an Ecosystem

The results of investigations carried out during the 44th and 50th cruises of the VITYAZ' forced us to revise the model of A. A. Lyapunov (Vinogradov et al., 1972; Vinogradov et al., 1973). The establishment of a significant role of bacteria in the process of energy transfer and the cycle of matter in the pelagic ecosystem (Sorokin, 1971a; and others) forced a new structural element to be added to the model--bacterioplankton. At the same time, it became necessary to consider the transfer of energy from phytoplankton to bacteria by means of dissolved organic matter (DOM). It was assumed that the excretion of DOM by phytoplankton represented 30% of its production. The intensity of

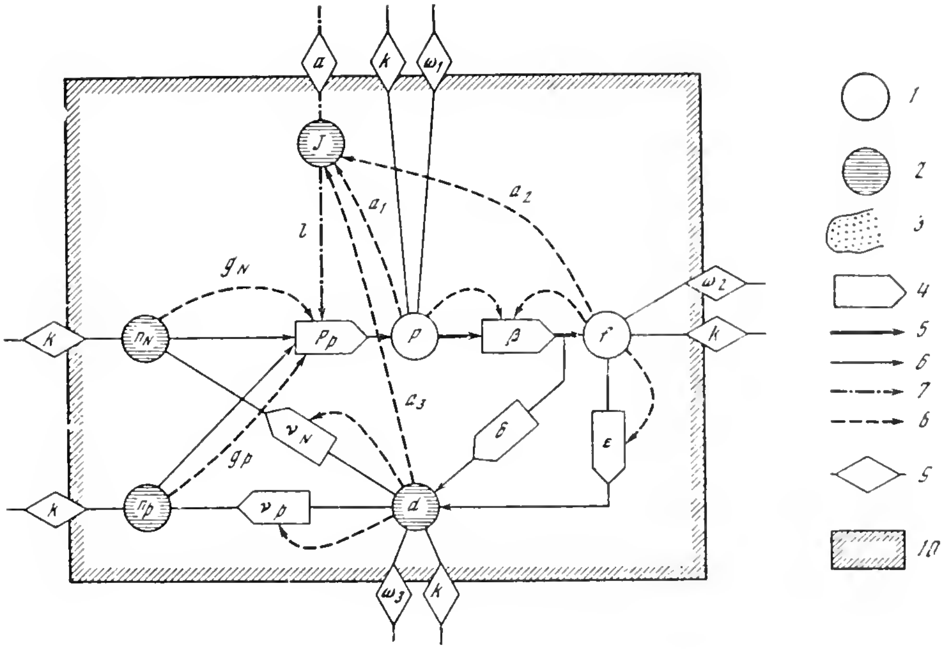


Fig. 1. Schematic diagram of a cell in the Lyapunov model. 1--animate element of ecosystem; 2--inanimate element of ecosystem; 3--group of elements in a cell; 4--flows of matter; 5--trophic connection; 6--transfer of matter; 7--energy of solar radiation; 8--information connection; 9--transport between cells; 10--a cell of the ecosystem; I--solar radiation; n_N--concentration of nitrogen; n_p--concentration of phosphorous; P_p--production of phytoplankton; P--biomass of phytoplankton; f--biomass of zooplankton; d--concentration of detritus (remaining symbols correspond to coefficients of equations 1.2-1.7 and are explained in text).

multiplication of bacteria was limited by the concentration of nutrient substances (detritus, DOM) and the limiting relationship of production to biomass.

The next refinement of the model of A. A. Lyapunov occurred when zooplankton stopped being considered as a single element, and became divided into Protozoa (f_1), microzooplankton (f_2), fine filter feeders (f_3), coarse filter feeders (f_4), small predators--cyclopoids (s_1), other small predators--calanoids (s_2) and large predators--chaetognaths and polychaetes (s_3). The Protozoa included Flagellata (heterotrophs), infusorians and radiolarians. The microzooplankton included the nauplii of copepods; the fine filter feeders (less than 1 mm) included such animals as the Oikopleura, Clausocalanus, Paracalanus, Acartia, Lucicutia, small Ostracoda, etc.; the coarse filter feeders (greater than 1 mm) included Undinula, Pleuromamma, Scolecithrix, Neocalanus, juvenile Euphausiacea, etc.

Many experimental data on the variation in the intensity of feeding of zooplankton with concentration of available food density forced us to abandon the plan of Vol'terra and begin use of the equation of V. S. Ivlev (1955). According to this equation, the relationship between the actual ration (C) and concentration of food (B) can be represented as:

$$C = C_{max}[1-e^{-\xi(B-B_0)}], \qquad (1.8)$$

where C_{max} is the maximum ration; B_0 is the minimum concentration of food, below which consumption ceases; ξ is a coefficient.

In establishing the selectivity of feeding in those cases when direct experimental data were not available, it was hypothesized that the concentration of a given type of food is proportional to its fraction in the actual ration. The mean daily rations (C) were calculated by the equation:

$$C = H + P + R = \frac{1}{U}(P + R), \qquad (1.9)$$

where H is the unassimilated food, P is the production, R is the rate of metabolism, U is the efficiency of assimilation. The values of R and U were determined directly in experiments (Shushkina, Vilenkin, 1971; Shushkina, Pavlova, 1973; Petipa et al., 1971; and others). The mean daily production was calculated by the equation: $P = RK_2/(1 - K_2)$, where K_2 is the coefficient of assimilated food used up for growth.

The equations related to the functioning of phytoplankton in the pelagic community were significantly refined, in comparison to the model of A. A. Lyapunov. An empirical ration was established (Voytov, Kopelevich, 1971) between the concentration of phytoplankton and detritus in the water and the light attenuation factor, which makes equation (1.2) more concrete:

$$a = 0.01 + 0.001(p + d). \qquad (1.10)$$

According to Ryther (1956), the variation in the intensity of photosynthesis with light flux I can be expressed as follows:

$$P'_p = P_{max}\frac{I}{I_{opt}}e^{(I - \frac{I}{I_{opt}})}, \qquad (1.11)$$

where I_{opt} is the light flux at which the maximum photosynthesis P_{max} is achieved. This relationship can be replaced by the following equation, which is closer to the empirical data:

$$P_p = P'_p(1 - 10^{0.1\ n_N})^{0.6}, \tag{1.12}$$

and has the same sense as the Michaelis-Menten equation.

In addition to limitations as to light and concentration of nutrients, the limitation of production of phytoplankton resulting from the maximum breeding rate was also considered.

In describing the hydrological situation, a three-layer model was used. In the surface layer ($0 \leqslant z \leqslant z_1$), high coefficients of turbulent diffusion were assumed: in the pycnocline ($z_1 \leqslant z \leqslant z_2$) the coefficient of turbulent diffusion decreased rapidly, and only at greater depths ($z > z_2$) did the intensity of mixing increase once more. The values of z_1 and z_2, defining the depth and thickness of the discontinuity layer are assumed in the model to be dependent on the time of development of the ecosystem (see Fig. 3).

The rate of natural descent of the phytoplankton (ω_1), bacteria (ω_2) and detritus (ω_3) are assumed to depend on the density of the water, which is determined by the vertical distribution of temperature and salinity.

Vertical migrations of a part of the zooplankton were simulated in the model so that the food requirements of the elements (f_4, s_1, s_2, s_3) inhabiting the 0-50 m layer are supplemented by a certain portion (K_m) of the total food requirements of the same elements located in the 50-150 m layer.

A schematic diagram of one cell of the model is shown in Figure 2, its spatial arrangement--in Figure 3. A water column was considered, extending from the surface to a depth of 200 m and divided into 20 elementary 10-meter cells. The relationship between cells located vertically one above the other was determined by the penetration of light (a), turbulent diffusion (k), sinking rate of phytoplankton (ω_1) and of detritus (ω_2). The daily input of light energy from the surface of the ocean (I_0) and the concentration of nutrients at 200 m depth (C_{200}) were assumed constant.

The horizontal displacement of the column of water was assumed to occur under the influence of a constant current with uniform distribution of velocity with depth. Vertical transfer of the water was by turbulent diffusion.

Under these assumptions, it becomes possible to replace the horizontal displacement of the water column containing the simulated ecosystem being modelled with the time of existence of the ecosystem from a certain initial state. In our case the initial state corresponded to the moment of ascent of the deep waters in the upwelling area.

It was assumed that in the initial state ($t = 0$), all elements of the simulated system were evenly distributed with respect to depth. The study of the model showed little sensitivity of the system to the

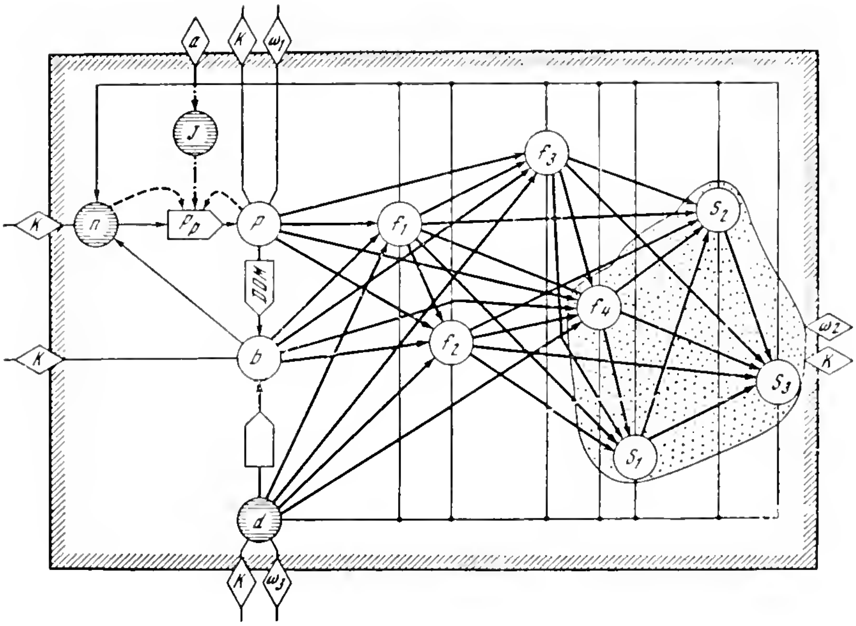


Fig. 2. Schematic diagram of a cell of the model considering the distribution of the elements of a pelagic ecosystem: J--solar radiation; P--biomass of phytoplankton; P_p--production of phytoplankton; n--concentration of nutrients; b--biomass of protozoa; f_2--biomass of microzooplankton; f_3--biomass of fine filter feeders; f_4--biomass of coarse filter feeders; s_1--biomass of cyclopoids; s_2--biomass of carnivorous calanoids; s_3--biomass of chaetognaths and polychaetes. DOM--dissolved organic matter. Remaining symbols same as in Figure 1.

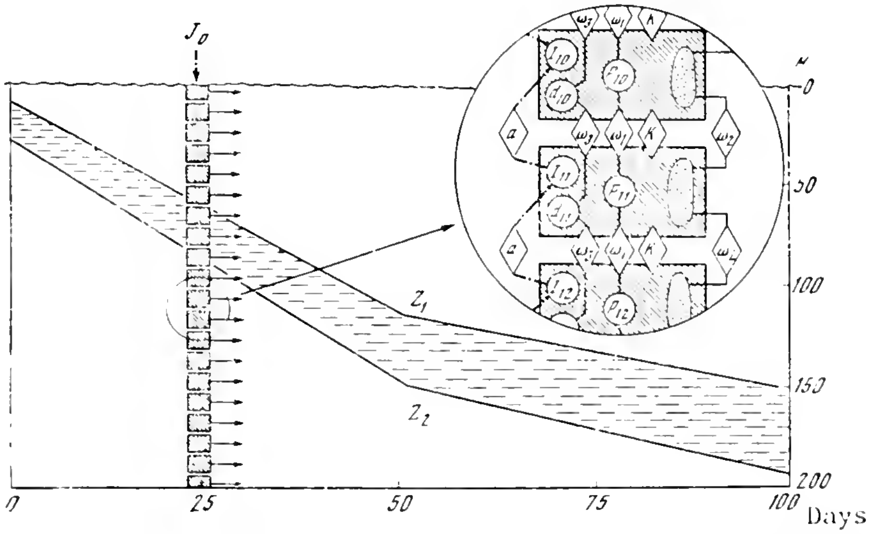


Fig. 3. Placement of cells of model simulating the vertical distribution of elements (horizontal shading marks area of pycnocline): symbols in circle same as in Figure 1.

selection of initial values of the biomass of the elements.

The system of equations of the model is as follows:

$$\frac{dI}{dz} = - aI \tag{1.13}$$

$$\frac{\partial n}{\partial t} = - hP_p + \nu d + \eta \sum R_i + K \frac{\partial^2 n}{\partial z^2} + \beta \frac{\partial n}{\partial z}$$

$$i = p_1, b_1, f \ldots f_4, \quad s_1 \ldots s_4 \tag{1.14}$$

$$\frac{\partial P}{\partial t} = \alpha P_p - R_p - \mu p - \sum C_{pi} + K \frac{\partial^2 p}{\partial z^2} - \omega 1 \frac{\partial p}{\partial z}$$

$$i = f_1 \ldots f_4 \tag{1.15}$$

$$\frac{\partial b}{\partial t} = P_b - R_b - \mu b - \sum C_{ij} + K \frac{\partial^2 b}{\partial z^2} - \omega 2 \frac{\partial b}{\partial z}$$

$$j = f_1 \ldots f_4 \tag{1.16}$$

$$\frac{\partial X_i}{\partial t} = u \sum C_{ji} - R_i - \mu i X_i - \sum C_{ij}$$

$$j = p_1, b_1, d_1, f_1 \ldots f_4, s_1, s_2 \quad j = f_2 \ldots f_4, \ s_1 \ldots s_3 \tag{1.17}$$

$$\frac{\partial d}{\partial t} = \sum (H_i + \mu i X_i) - \sum Cd_i + K \frac{\partial^2 d}{\partial z^2} - \omega 3 \frac{\partial d}{\partial z}$$

$$i = f_1 \ldots f_1, s_1 \ldots s_3 \quad i = f_1 \ldots f_4, \tag{1.18}$$

where η is the coefficient of nutrient release in the process of metabolism, as a fraction of the utilization of nutrients in metabolism ($\eta = 0.05$); C_{ij} is the specific ration of the ith food consumer represented by the jth food source; μ is the natural mortality coefficient; X_i is the biomass of the ith zooplankton element ($i = f_1$, f_2, f_3, f_4, s_1, s_2, s_3); H_i is the nonassimilated food of the ith zooplankton element.

$$H_i = (1 - u_i) \sum C_{ji}$$

$$j = p, \ b, \ d, \ f, \ s.$$

The remaining symbols are explained above or are analogous to the symbols used in the model of A. A. Lyapunov (equations 1.2-1.7).

The system of equations of the model was reduced to a finite-difference plan with a time step of one day, a depth step of 10 m.

Figure 4 shows the change in biomass of elements of this system with the passage of time and, consequently, increasing distance from the zone of the water ascent. The biomass of phytoplankton and bacteria increased most rapidly. The fine filter feeders lagged somewhat in their development, coarse filter feeders developed still more slowly, their biomass reaching its maximum only on day 30 of existence of the system. Nevertheless, their combined effect on phytoplankton and bacterial plankton, in addition to the retarded growth of the bacterial plankton due to exhausting the reserves of biogens, leads to a sharp decrease in the biomass of phytoplankton and bacterial plankton. The inertia of the predators is still greater than that of the filter feeders: the biomass of the various groups of predators reaches its maximum only on day 35-50 of existence of the community.

On day 50-60, the system reaches a state which is near steady. It is characterized by low biomass of living elements and balance between production and consumption of phytoplankton. This mature state of the community typically shows little variability of the elements with further passage of time and, consequently, little variability in space, and is the state observed in oligotrophic water areas in the tropical regions of the ocean, particularly the halistatic zones of the planetary convergences.

The model data agree qualitatively quite well with data obtained by observation in the ocean. A comparison of the values of biomass of the elements of the ecosystem obtained from the model with those observed in the field is presented in Table 1. Considering the relative coarseness of the model, its agreement with the original can be considered acceptable.

The model changes in vertical distribution of the elements of the ecosystem with time are presented in Figure 5. During the early period (t = 5 days), when the total quantity of phytoplankton was almost maximal, its biomass was evenly high in the 10-50 m layer. All the other living elements of the ecosystem have a more or less sharply expressed maximum, related to the thermocline. However, by the 10th day the reserve of nutrients in the upper layer was almost completely exhausted, while at a depth of 10-20 m the maximum biomass of the phytoplankton was still retained. Deeper, at the upper boundary of the thermocline, nutrients passing through the thermocline began to form a second, lower, maximum, which was still poorly expressed. This dual-maximum structure is characteristic for the vertical distribution of almost all elements of the ecosystem (Vinogradov et al., 1971).

As the stock of nutrients in the surface layer decreased, the vertical transfer of nutrients from beneath the discontinuity layer continued to play an increasingly significant role in the functioning of the ecosystem. The lower maximum of biomass of phytoplankton became greater than the upper maximum. As the thermocline continued to descend to 80-100 m and deeper, the illumination at its upper boundary became

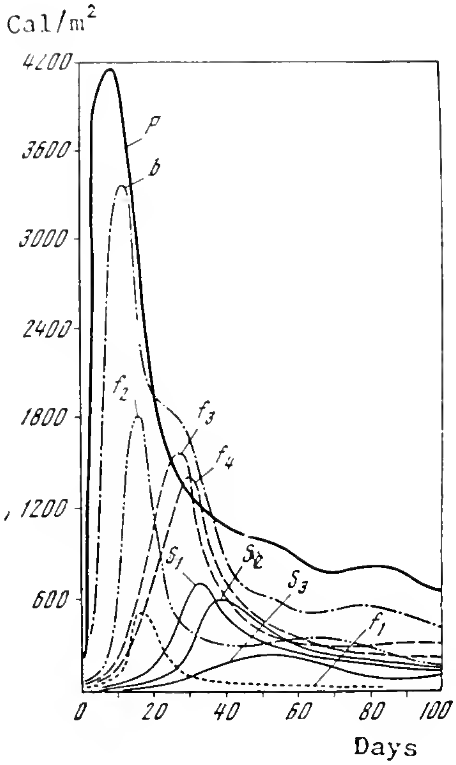


Fig. 4. Change of total biomass of living elements of a pelagic ecosystem from the tropical regions of the ocean in the 0-150 m layer: P--phytoplankton; f_1--Protozoa; b--bacterioplankton; f_2--microzooplankton; f_3, f_4--fine and coarse herbivores; s_1--Cyclopoida; s_2--carnivorous Calanoida; s_3--Chaetognatha and Polychaeta.

insufficient for intensive development of phytoplankton. A situation was created in which the lower maximum "separated" from the thermocline, and its position was subsequently determined by the lower limit of illumination and the flow of nutrients from deeper levels.

With still more mature state of the community (over 60-80 days), in the oligotrophic and ultraoligotrophic regions, according to the model, almost complete disappearance of the upper maximum of all elements should occur. Actually, the upper maximum disappears only for the phytoplankton, continuing to exist for the zooplankton even in oligotrophic regions. An analogous picture is yielded by several modernized versions of this model (Vinogradov et al., 1975).

The results produced show that many of the existing features of vertical and time distribution of elements in the pelagic ecosystem of the tropical regions of the ocean can be quantitatively reproduced and explained by means of the model described. However, many important aspects of the functioning of pelagic ecosystems still remain outside the model. The assumption of constancy of the velocity vector of a current in the 0-200 m layer and resulting absence of horizontal displacements hardly agrees with the picture actually observed in the ocean. Finally, the model developed fails to consider the final trophic

Table 1. Biomass (cal/m^2) of the elements of the system in the 0-150 m layer (Vinogradov et al., 1973).

Element	Community of low maturity (ages 30-40 days)			A more mature community (ages 60-80 days)	
	Model Data		VITYAZ', 4°30' S 142°30' E	Model Data	VITYAZ', 13° N, 140° E
	Day 30	Day 40	Days 30-40	Day 80	Days 60-80
Phytoplankton (p)	1,319	1,092	2,000	827	900
Bacteria (b)	1,673	864	4,100	564	2,180
Nauplii (f_2)	394	303	321	300	?
Fine Filter Feeders (f_3)	1,338	612	525	290	74
Coarse Filter Feeders (f_4)	1,416	726	420	252	164
All herbivores	3,184	1,641	1,266	842	?
Cyclopoida (s_1)	624	491	495	203	236
Calanoida (s_2)	288	600	610	191	175
Chaetognatha (s_3)	184	183	15	102	51
All carnivores	1,096	1,274	1,120	496	462

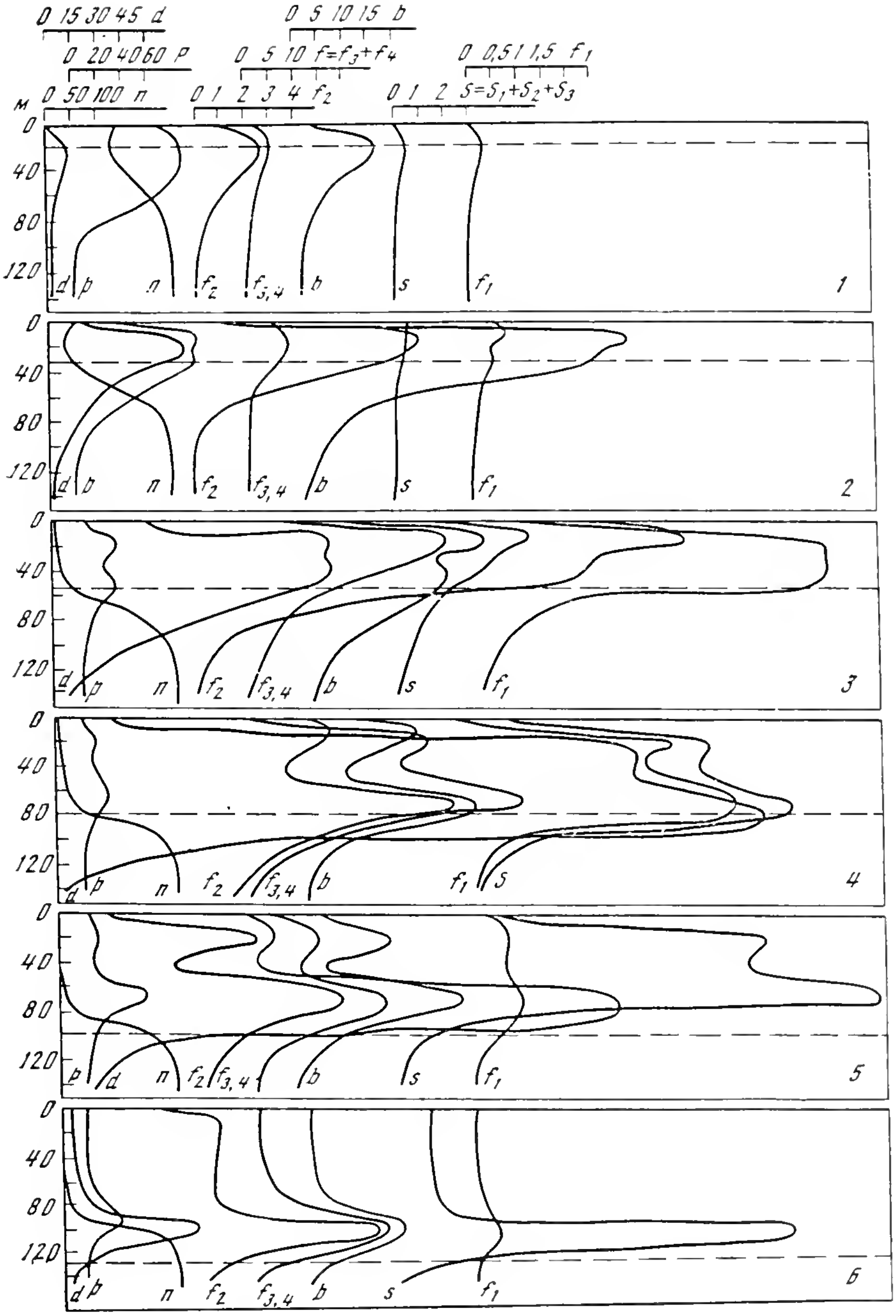


Fig. 5. Changes in vertical distribution of elements of an ecosystem for moments in time (t = 5 (1), 10 (2), 20 (3), 30 (4), 40 (5), and 60 (6) days): vertical line shows depth, m. Horizontal dotted line shows upper boundary of thermocline; n = nutrients, other symbols same as in Figure 4. Note the difference in scales used for the different elements.

links in the chain--fish, cephalopods, and aquatic mammals, which are of the greatest interest from the standpoint of their utilization.

Let us analyze some other approaches to the construction of simulation models of pelagic ecosystems.

1.3. Model Considering the Distribution of Elements by Area

The modelling of changes in the pelagic ecosystem not in depth, as was done in the previous section, but rather over the area of a body of water, can serve as another approximation of reality. This approach is particularly important for water areas with a complex system of surface currents and various faunistic groups in the plankton.

The prototype for the creation of a model considering the distribution of elements over a water area (Menshutkin et al., 1974) was the Sea of Japan, in which, due to the sparsity of shallow zones, we can separate the open part of the sea as an independent pelagic ecosystem. The strong but inconstant flow of water through Tsushima Strait creates significant horizontal heterogeneities, justifying the model type selected. In addition to the passive transfer of hydrobionts with the current, nektonic animals actively migrate through Tsushima Strait--squid and fish--entering the Sea of Japan in the spring and summer and leaving it in the winter.

To make the model more concrete, ecologic-faunistic characteristics of the plankton of the Sea of Japan and data on the trophic relationships among the primary groups of its population, obtained during the 52nd cruise of the VITYAZ' and a number of shoreline expeditions, were used (Pasternak, Sushkina, 1973; Sushkina, 1972).

In constructing the model, the entire water area of the sea was divided into squares 150 km on a side. Each square corresponds to an elementary cell of the ecosystem, in which the volume of water down to a depth of 200 m is studied. Within each cell, the heterogeneities of horizontal distribution of abiotic and biotic elements are assumed to be insignificant.

The transfer of dissolved matter or suspended particles of detritus, phytoplankton and zooplankton from one cell into another results from the currents. A diagram of the currents presented by I. V. Sizova (1961) was accepted, with the loss of detail resulting from the size of the cells. Seasonal changes in the speed of the Tsushima Current, following S. Nishimura (1969), were considered sinusoidal with a maximum in September. The effective temperature (mean water temperature at which the population of a given species finds itself in a given cell) was assumed to be a function of time and the coordinates of the cell, while the temperature field was taken from S. Nishimura (1969).

Each cell of the model of the ecosystem contained twelve elements (Fig. 6). The group of inanimate elements was represented by the concentrations of nutrients (n) and detritus (d). Plankton was divided

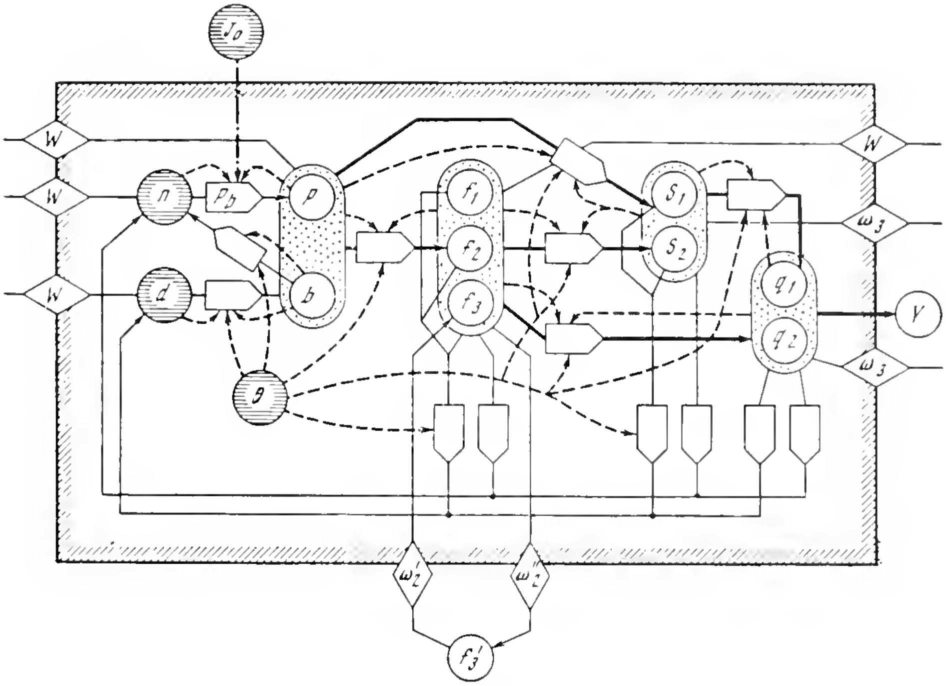


Fig. 6. Schematic diagram of a cell of the pelagic ecosystem of the Sea of Japan: J_0--solar radiation; n--nutrient concentration; p--phytoplankton; b--bacterioplankton; d--detritus; f_1--boreal herbivorous epiplankton; f_2--warm-water herbivorous epiplankton; f_3--interzonal herbivorous zooplankton; s_1--carnivores of the boreal complex; s_2--carnivores of the warm-water complex; q_1--fish; q_2--squid; θ--water temperature; W--transport by currents; Y--catching of fish and squid, ω_3--active migrations of fish and squid; ω'_2, ω''_2--seasonal vertical migrations of interzonal plankton.

into three groups of organisms: microplankton, mesoplankton I (herbivores) and mesoplankton II (carnivores and omnivores). The composition of the microplankton included phytoplankton (p) and bacterioplankton (b). Mesoplankton I included boreal epiplankton f_1, warm-water epiplankton f_2 and interzonal plankton f_3. The seasonal vertical migrations of interzonal herbivores were considered, and a special element was distinguished--the wintering stock (f'_3)--interzonal zooplankton which spends the winter at depths greater than 200 m. It was assumed that the wintering stock is not moved by the surface system of currents. Two elements were distinguished among the mesoplanktonic carnivores and omnivores: species of the boreal comples (s_1) and species of the warm-water complex (s_2).

In contrast to the planktonic elements, passively transported from cell to cell by currents, the elements of the nekton (fish--q_1 and squids--q_2) can move actively. For lack of a better hypothesis, it was assumed that the fish and squids search out the maximum of food in the cell in which they are located in neighboring cells. The rate of movement of fish was assumed to be 10 km/day, of squids 15 km/day.

One peculiarity of the model in question is that the elements of the cells of the ecosystem are combined into groups. A group includes elements with similar dimensions of individuals, type and spectrum of feeding, and interaction with predators. Essentially, the organisms combined into a group occupy a single, broad ecologic niche. However, the reaction to abiotic factors, energy characteristics and peculiarities of migration remain specific for each such element. This separation of trophic groups greatly simplifies the modelling algorithm and does contradict the biologic essence of the process being modelled. The time step of functioning of the model was 5 days.

Operation of the model began with an arbitrary initial state, assuming even distribution of all elements of the ecosystem over the water area of the sea. After three years, functioning of the model led to a state which was near steady, in which the difference in the states of the elements of the ecosystem for any given date of any two years did not exceed 10%.

The data, averaged over the entire surface of the Sea of Japan, on monthly production of phytoplankton and zooplankton, bacteria and nekton show that the production of phytoplankton has two rather sharp maxima. The mean annual production of phytoplankton of the entire Sea of Japan, according to the model, is 1,280 kcal/m^2 per year--a quantity which is quite probable, judging from the data of Yu. I. Sorokin and O. I. Koblentz-Mishke (1958). It is difficult to evaluate the likelihood of the values of production of bacterioplankton and zooplankton obtained in the model due to the lack of field determinations. The production of the higher trophic levels (commercial fish and squid) can be compared with their catch levels (Moiseyev, 1969). According to the model, the annual fish catch (30% of the ichthiomass present), with a calorie content of 1 kcal/g of wet mass, would be 820,000 tons for the entire Sea of Japan, of squid--540,000 tons. The actual fish and squid catch is about 1,000,000 tons, the potential possible catch--about 1.23 million tons (Gulland, 1970).

The distribution of biomass of phytoplankton over the water area of the Sea of Japan, according to the model data, is shown in Figure 7. In the winter there are only small accumulations of phytoplankton along the coast of Japan in the region of the Noto Peninsula and further south. Intensive vernal development of phytoplankton occurs in Petr Velikiy Bay and the entire central portion of the sea. By summer, the area covered by accumulations of phytoplankton is reduced and is divided into two areas--along the coast of Japan and Primor'ye. In the fall, the eastern and central portion of the sea contains high phytoplankton biomass.

Boreal epiplankton in the uper 200 meter layer is quite sparse during the winter months. In the spring (March) the water area of high concentration is significantly expanded and in the summer (July), the area with a biomass of over 1 kcal/m^2 covers almost all of the northeastern portion of the sea, including Petr Velikiy Bay.

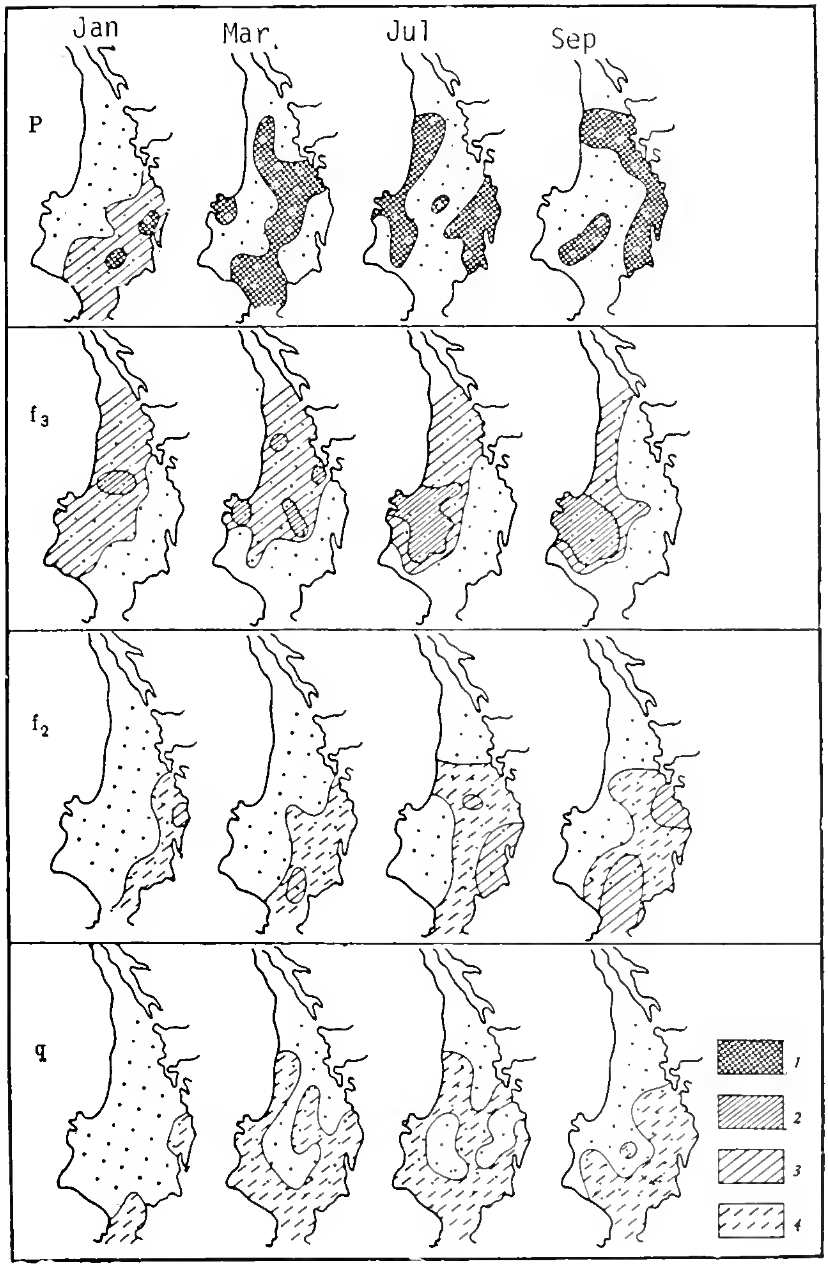


Fig. 7. Model maps of the distribution of certain elements of the ecosystem of the pelagic zone of the Sea of Japan: P, phytoplankton; f_3, interzonal herbivores; f_2, herbivorous and omnivorous zooplankton (southern forms); q, nekton (fish and squid); 1, biomass kcal/m^2; 1, > 10; 2, 10-5; 3, 5-1; 4, 1-0.1. Points represent centers of cells of the model.

Interzonal herbivores, which make up the main mass of the summer plankton, are rather evenly distributed in the winter over depths of more than 200 m throughout the entire cold-water portion of the sea. In the spring, they migrate to the surface layer, where their biomass rapidly increases, and in the summer, over most of the water area, their biomass is at least 5 kcal/m^2 (Fig. 7). The seasonal dynamics of the spatial distribution of the boreal omnivorous mesoplankton, in its most general features, repeats the distribution of interzonal herbivores, but with significantly lower biomass.

The distribution of southern forms of zooplankton (Fig. 7) is determined basically by the temperature conditions and mode of the Tsushima Current. In winter, their main mass is concentrated along the coast of Japan. In spring, heating begins and the arrival of warm water and zooplankton from Tsushima Strait increases, reaching its maximum in fall. As a result, during the fall the area of distribution of the southern forms of zooplankton covers almost the entire southeastern portion of the sea.

The migration of nektonic animals (fish and squid) begins in the spring in the southern portion of the Sea of Japan and follows 2 main tracks: the more numerous stream is directed along the Honshu coast to the northeast, the less numerous stream--along the coasts of Korea toward Petr Velikiy Bay. In the summer and fall, significant numbers of squid, according to the data from the model, are observed in the central portion of the sea in the zone of contact between the Primorskiy and Tsushima Currents (Fig. 7).

Unfortunately, there are no sufficiently complete data available on the true distribution of the biomass of phytoplankton, bacterioplankton and zooplankton, fish and squid in the water area of the Sea of Japan in the seasonal aspect. Therefore, the question of the degree of accuracy of the model which has been created remains open, although we can note that the picture of distribution of zooplankton obtained in the model is not contradicted by the available (though rather fragmentary) observations of the distribution of its biomass. The distribution of squid also agrees in general terms with the observed distribution (Zuyev, Nesis, 1971).

The model in question shows the actual possibility of quantitative description of the seasonal changes and distribution over a water area of elements of a pelagic ecosystem. Obviously, models of this type can yield not only production, but also zoogeographic information. The separation of species of boreal and warm-water complexes in the model of the Sea of Japan is a step in this direction.

It must be considered that models of this type are quite sensitive to the quality of hydrologic data used. The need not only for a general diagram of currents, but also for values of mass transfer in each square of the water area, as well as precise values of the coefficient of horizontal turbulent diffusion, places certain limitations on the area of application of such models.

1.4 Model Simulating the Volumetric Distribution of Elements

The transition to three-dimensional models is a natural development of the models discussed above. This transition is particularly necessary upon analysis of upwelling zones or areas of the ocean with strong subsurface countercurrents. Let us study the ecosystem of the eastern portion of the equatorial Pacific, where we encounter a complex and unique structure of the field of currents. To represent the situation which has developed there as a plane model would be an unjustified simplification. On the other hand, we do not have sufficiently complete information concerning the field of currents and coefficients of turbulent diffusion in this region of the ocean. Therefore, we must, for now limit ourselves to a very simplified, approximate plan, which is more qualitative than quantitative in nature.

Figure 8 shows a block diagram of an elementary cell of the model and the location of the cells in space. Keeping in mind the qualitative nature of the model, the structure of the trophic network of a cell has been greatly simplified and includes nutrient salts (n), detritus (d), phytoplankton (P), bacterioplankton (b), herbivores (f), and carnivores (s).

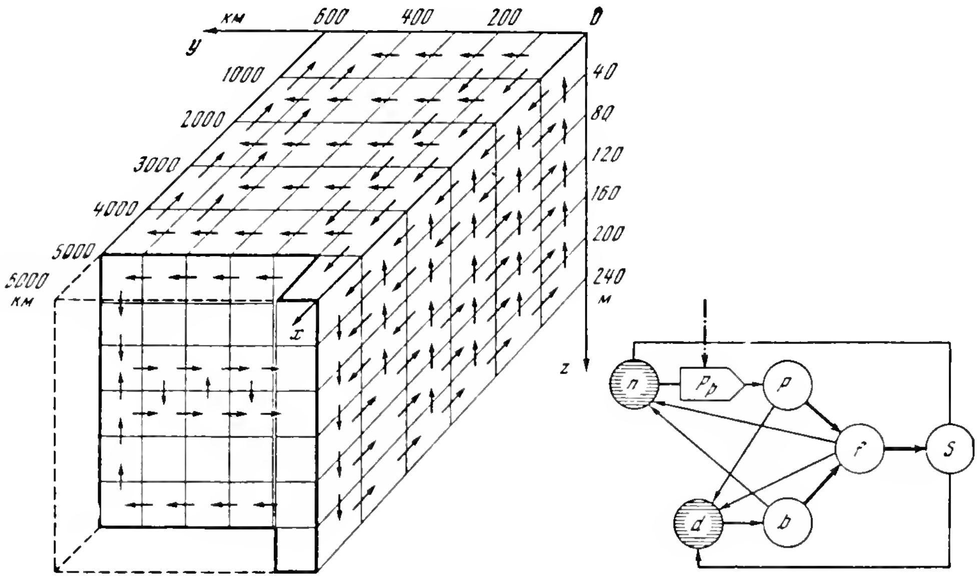


Fig. 8. Block diagram of 3-dimensional model of pelagic ecosystem and 3-dimensional placement of cells of the model. Arrows show transfer by currents. In the box, we show the relationship between concentration of nutrient salts (n), phytoplankton (P), bacterioplankton (d), detritus (d), herbivores (f), and carnivores (s).

In all, there are 216 elementary cells in the model, forming a parallelepiped, extended along the equator. The distance between the centers of cells in longitude (X axis) is 1,000 km, in latitude (Y axis)--100 km, in depth (Z axis)--40 m. The system of currents was selected so as to imitate the surface trade current (along the X axis from the coordinate origin) and the Cromwell current, gradually approaching the surface (directed parallel to the X axis, but toward the coordinate origin). In the immediate vicinity of the equator (plane XZ), there is a significant vertical component to the velocity of the flow, leading to ascent of waters to the surface.

The surface current, directed toward the coordinate origin and flowing parallel to the X axis some 500-600 km to the north of the equator, imitates the equatorial countercurrent, in the area of which we find the convergence zone. The model imitates the outflow of surface waters away from the equator (movement along the Y axis from the coordinate origin) and the corresponding deep countercurrent (parallel to the Y axis toward the coordinate origin). The maximum vertical component of speed of the flow is equal to 5 m/day ($0.6 \cdot 10^{-3}$ m/s), while the maximum horizontal speed is 50 km/day. The diagram of the currents was selected so that the condition of continuity is maintained for each cell. The model considers the transfer of elements of the currents and the gravitational precipitation of detritus.

The initial state of the model was assigned in the form of an even distribution of all elements throughout the entire volume analyzed. After 30-40 days of the transient process, the model approached a stable state, in which the flow of biogenic salts toward the bottom surface of the parallelepiped was balanced by precipitation of detritus through this surface.

The maximum concentration of phytoplankton is created in the area of the maximum intensity of upwelling (coordinate origin). As we move along the X axis (along the equator toward the west), the concentration of phytoplankton decreases, while the maximum itself descends to a depth of 80 m. This result agrees both with observations at sea, and with data obtained in a 2-dimensional model.

The distribution of biomass of herbivores is characterized by the formation of two areas of concentration: one is located on the equator to the west of the region of intensive upwelling, while the second is extended in the latitudinal direction north of the equator in the convergence zone. It is characteristic that the maximum concentration of phytophages is deeper in the zone of the convergence.

The area of predominance of carnivores is extended in a broad strip from east to west in the zone of the northern trade current. The maximum concentration of predaceous zooplankton is found at a depth of 60-120 m. In the stable state of the model, the carnivores are distributed almost throughout the entire volume down to a depth of 200 m, which is less typical of herbivores and not at all typical of phytoplankton.

A comparison of the distribution of elements of the model with observed data in the equatorial portion of the east Pacific (Vinogradov, Voronina, 1963; Voronina, 1964; Blackburn et al., 1970) shows qualitative agreement of the distribution of phyto- and zooplankton in the model and in the field. The decrease in the concentration of phytoplankton to the west as we move along the equator appeared rather clearly in the model, in spite of its approximate nature. The maximum of predaceous zooplankton in the area of the convergence at 5°N is also noted in the model although another maximum of carnivores, on the equator between 150 and 160°W, is almost not reflected in the model. It is possible that this is related to the elevated values of horizontal flow speeds in the model, or to the fact that only predators with characteristic dimensions of not over 10 mm were analyzed.

This model, despite its extreme sketchiness and the qualitative nature of results produced, demonstrates the genuine possibility of creating 3-dimensional models of pelagic ecosystems in the ocean. However, the experience of development of models of this type has shown that there are significant difficulties. First of all, clarification of the 3-dimensional field of the velocity vector of a current, even for steady conditions, is a complex, cumbersome and, at the present time, sometimes impossible hydrophysical task. Secondly, to ignore processes of turbulent transfer, as this model does, is possible only as a first approximation. Consideration of horizontal and vertical turbulent transfer, however, would introduce new complications. In 3-dimensional models, consideration of the active movements of zooplankton and, particularly nekton, becomes extremely necessary, greatly complicating them in comparison to 1-dimensional and plane models.

2. Stochastic Models of Communities. (B. S. Fleishman)

A community is a complex open stochastic system (Fleishman, 1976), but its deterministic models are justified in the first approximation by the law of large numbers.

There is an extensive literature on deterministic dynamic models of community, based on differential, finite-difference and matrix equations.

A community consists of components--populations or groups of populations, distinguished according to some principle. The individuals of component α, in turn, may form a stable formation of n_α individuals. This formation will be called an α-individual. Their number in a certain biotope of volume V will be represented by N_α. The density of the α-individuals (density of the biomass) will be denoted by the expression $\rho_\alpha = N_\alpha/V$ ($B_\alpha = \rho_\alpha\beta_\alpha$), where $\beta_\alpha = n_\alpha\beta'_\alpha$ is the mean biomass of an α-individual, β'_α is the mean biomass of an individual of the α-component.

Theoretically, we can divide a biotope of volume V into N elementary cells of volume ΔV, occupied by only one α-individual or empty. Suppose $V_\alpha = \Delta V N_\alpha$ is the volume occupied by α-individuals, while $V_{a+1} = \Delta V N_{a+1}$ is an empty volume with N_{a+1} elementary cells

$$\left(\sum_{\alpha=1}^{a+1} N_\alpha = N\right).$$

If we analyze a stochastic model of a community without considering the aggregation of α-individuals, i.e., if we consider all placements of the N_α α-individuals in the N cells equally possible, then the probability of presence of an α-individual in any cell (probability of an α-individual) is equal to $p_\alpha = N_\alpha/N$, while the probability of an empty cell is equal to $p_{a+1} = N_{a+1}/N$. It is easy to show that the probabilities are proportional to the densities $p_\alpha = \rho_\alpha \Delta V$. However, the introduction of probabilities is important, due to the possibility of working with them and using the apparatus of the theory of probabilities.

Thus, the status of a community is described by a probabilistic vector $p = (p_\alpha)$. If the αth component of the community consists of one population, it can be divided into b_α age groups, considering $p_\alpha = (p_{\alpha s})$ to be a vector, where $p_{\alpha s}$ is the probability of α-individuals of the sth age group.

2.1 Dynamic Model of a Community Ignoring Aggregation

The succession of a community (Odum, 1975) can be described by a stochastic model with discrete time $t = 1,2,\ldots.$ The time step taken as unity corresponds to the characteristic time interval for the community in question: a day, a month, a year. The status of the community at moment in time $t+1 p^{t+1}$ in the model in question can be represented as follows:

$$p^{t+1} = p^t P_t, \qquad (2.1)$$

where $P_t = ||P^t_{\alpha\beta}||$ $(\alpha,\beta = \overline{1,\alpha})$--is a stochastic matrix. In order to consider the effect of delay in the reaction of the community, we can require that the probabilities $p^t{}_{\alpha\beta}$ depend on the k states $p^{t-k},\ldots p^{t-1}$, preceeding state t.

$$p^t_{\alpha\beta} = p^t_{\alpha\beta}(p^{t-K},\ldots,p^{t-1}) \quad \text{or} \quad P_t = P_t(p^{t-k},\ldots,p^{t-1}). \qquad (2.2)$$

The specifics of each community, related to the trophic and tropical structure of interactions of its components, as well as its interaction with the environment, is described by the unsteady equations (2.2). Recording of these data, together with the k first states $p^1,\ldots,p^k$, unambiguously defines all subsequent states of the community. However, certain modifications of these interactions are always possible, which ecologists consider permissible within a given community (not leading, from their point of view, to a new community). In our model, this is formalized by the assignment of a certain set W_a of permissible functional transforms (2.2), describing the very same community.

A climax community (Odum, 1975) corresponds to the limiting behavior of the model as $t\to\infty$. The limiting state $p = \lim_{t\to\infty} p^t$ exists if there is a limit $P(.,\ldots,.) = \lim_{t\to\infty} P_t(.,\ldots,.)$, corresponding to steady influence of the environment and relationships within the community in the climax state. The limiting state is independent of the k initial states and can be found from the equation

$$p = pP(\underbrace{p,\ldots,p}_{k}) \qquad (2.3)$$

It is convenient to find the solution of this equation in two stages. In the first stage, we seek out the solution of the linear, homogeneous equation $p = p||p_{\alpha\beta}||$ to express p through $p_{\alpha\beta}$

$$p = F[p_{\alpha\beta}] \qquad (2.4)$$

In the second stage, we solve the transcendental equation

$$p = F[p_{\alpha\beta}(\underbrace{p,\dots,p}_{k})] \qquad (2.5)$$

for p. In accordance with what we said above, the community at climax corresponds to the set $U=\{\|p_{\alpha\beta}\|\}$ of limiting values, corresponding to the permissible set $W_a=\{p_{\alpha\beta}(\cdot,\dots,\cdot)\}$ of the functional transforms $p_{\alpha\beta}(\cdot,\dots,\cdot)$. We note that a portion of the functions $p_{\alpha\beta}(\cdot,\dots,\cdot)$ may be independent of p.

Let us analyze an explicit solution of the equations presented for the model of the community, based on the characteristics of birth and death of α-individuals. These characteristics, as resultant indices of interactions of the components of the community among themselves and with the environment, are widely used, primarily for the description of the higher trophic levels of community.

Let us introduce the conditional probability of birth $\lambda^t_{\alpha s}$, and the conditional probability $\mu^t_{\alpha s}$ of death of an α-individual of the corresponding age in one time step.

It can then be shown that:

$$P_t = \begin{pmatrix} \mathbf{p}^t_{11} & & & & p^t_{1a+1} \\ & \ddots & & 0 & \vdots \\ 0 & & \mathbf{p}^t_{\alpha a} & & p^t_{\alpha a+1} \\ & & & \ddots & \vdots \\ & & & \mathbf{p}^t_{aa} & p^t_{aa+1} \\ p^t_{a+11} & \cdots & p_{a+1\alpha} & \cdots \; p_{a+1a} & p_{a+1,a+1} \end{pmatrix} \qquad (2.6)$$

$$p^t_{a+1\alpha} = (\underbrace{\lambda^t_\alpha, 0, \dots, 0}_{b_\alpha}), \qquad p^t_{a+1,a+1} = 1 - \sum_{\alpha=1}^{a} \lambda^t_\alpha.$$

$$p^t_{\alpha\alpha} = \begin{pmatrix} 1-\mu^t_{\alpha 1}-\lambda^t_{\alpha 1}\lambda^t_{\alpha 1} & & & & \\ & \ddots & \ddots & & 0 \\ & & 1-\mu^t_{\alpha s}-\lambda^t_{\alpha s}\lambda^t_{\alpha s} & & \\ & & & \ddots \quad \ddots & \\ 0 & & & 1-\mu^t_{\alpha b_\alpha -1}-\lambda^t_{\alpha b_\alpha -1}\lambda^t_{\alpha b_\alpha -1} & \\ & & & & 1-\mu^t_{\alpha'_\alpha} \end{pmatrix}, \qquad p^t_{\alpha a+1} = \begin{pmatrix} \mu^t_{\alpha 1} \\ \vdots \\ \mu^t_{\alpha s} \\ \vdots \\ \mu^t_{\alpha b_\alpha -1} \\ \mu^t_{\alpha b_\alpha} \end{pmatrix}$$

Equation (2.4) in this case has a simple solution:

$$p_{\alpha s} = \frac{\lambda_\alpha}{\lambda_{\alpha 1}+\mu_{\alpha 1}} \prod_{u=2}^{s} \frac{\lambda_{\alpha u-1}}{\lambda_{\alpha u}+\mu_{\alpha u}} p_{\alpha+1}, \quad p_{\alpha+1} = \left(1 + \sum_{\alpha=1}^{\alpha} \sum_{s=1}^{b_\alpha} \frac{p_{\alpha s}}{p_{a+1}}\right)^{-1}. \qquad (2.7)$$

complete solution of system (2.7) requires explicit assignment of the variation of λ^t_α , $\lambda^t_{\alpha s}$ and $\mu^t_{\alpha s}$ with $p^t_{\alpha s}$ and the parameters of the environment. In addition to the variations which are specific for each community, at least the following two are common. Suppose the conditional probabilities λ^s_α of birth of α-individuals of the first age group from α-individuals of age groups (probabilities of fertility by ages) are assigned.

Then:

$$\lambda^t_\alpha = \sum_{s=1}^{b_\alpha} \lambda^s_\alpha p^t_{\alpha s} \ . \qquad (2.8)$$

On the other hand, suppose the death of α-individuals, defined by the probability $\mu^t_{\alpha s}$, depends on K independent events--both in the environment and within the biocenosis (catastrophies, fishing, predators, parasites, food shortages, natural death, etc.). The probability of these fatal events is represented as $\mu_{\alpha sk}$ $(k=\overline{1,K})$. Some of them, in turn, may depend on the status of the system p^t.

Then, as we can easily demonstrate:

$$\mu^t_{\alpha s} = \{1 + [\sum_{k=1}^{K} (\mu^{-1}_{\alpha sk} - 1)^{-1}]^{-1}\}^{-1} \ . \qquad (2.9)$$

We note that only where $\mu_{\alpha sk} < c \ll 1$ does approximate additiveness occur:

$$\mu^t_{\alpha s} = \sum_{k=1}^{K} \mu_{\alpha sk} + 0\,(c) \ , \qquad (2.10)$$

which, as a rule, is not considered in the ecologic literature.

Let us study a few particular cases of the relationships we have derived. Let us begin with the case of a single population (a=1), divided into b_1 age groups. Using equations (2.1) and (2.6) in our case, we produce, for the probability of the first age group

$$p^{t+1}_{11} = p^t_{11}(1 - \mu^t_{11} - \lambda^t_{11}) + p^t_2 \lambda^t_1 \ . \qquad (2.11)$$

We will consider that the reproductive capacity is equal only for age groups beginning with group s_0. Mathematically, this can be expressed as:

$$\lambda_1^s = \begin{cases} 0 & \text{for } 0 \leqslant s \leqslant s_0 - 1 \\ f & \text{for } s_0 \leqslant s \leqslant b_1 \end{cases} \tag{2.12}$$

Furthermore, we will assume the quantity f, which characterizes this reproductive capacity, to be a function of the summary probability

$$S_t = \sum_{s=s_0}^{b_1} p_{1s}^t$$

of the reproductive age groups. Then, equation (2.11), considering (2.8) and 2.12), can be rewritten as:

$$R_{t+1} = S_t f(S_t),$$

where $$R_{t+1} = \{p_{11}^{t+1} - p_{11}^{t}(1-\mu_{11}^{t} - \lambda_{11}^{t})\}/p_2^t$$

has the sense of "supplementation," while S_t has the sense of a "reserve." Recurrent equations of this type are widely used in the literature without a probabilistic basis. A basis is developed for them using a deterministic matrix model developed by Lesley in the book *Fish Stocks and Recruitment* (1970); for $f(S)=\alpha\exp(-\beta S)$, a Ricker model is available, while for $f(S)=(\alpha S+\beta)^{-1}$ the model of Beverton and Holt can be used, or α and β are constants (Beverton, Holt, 1957).

The remainder of our brief presentation concerns the case of an a-component community (a>1) with components not divided into age groups ($b_\alpha=1$). Representing $\mu_{\alpha 1}=\mu_\alpha$ and $p_{\alpha 1}=p_\alpha$, using equation (2.7) for the steady case, we obtained:

$$\left.\begin{aligned} p_\alpha &= \frac{\lambda_\alpha}{\mu_\alpha} p_{\alpha+1} , \\ p_{\alpha+1} &= \Big(1 + \sum_{\alpha=1}^{\alpha} \frac{\lambda_\alpha}{\mu_\alpha}\Big)^{-1} \end{aligned}\right\} . \tag{2.13}$$

For the remainder of our presentation, the particular case of equation (2.9) when K=2 is important:

$$\mu_\alpha = \mu(x_\alpha, y_\alpha) = \frac{x_\alpha + y_\alpha - 2x_\alpha y_\alpha}{1 - x_\alpha y_\alpha} \ (\alpha = \overline{1, \alpha}), \tag{2.14}$$

where x_α and y_α are the probabilities of death of an α-individual due to causes inside and outside the community, respectively.

2.2 Model Study of Optimal Strategies of a Community.

The structure of a community in our model is defined by the vector $x=(x_\alpha)$ of the death of an α-individual from causes within the community, particularly natural death related to the trophic structure, etc. Obviously, it is less variable with time than is the vector $\lambda=(\lambda_\alpha)$ of birth of α-individuals. Therefore, vector x will be considered a fixed parameter of the model while vector λ, defining the behavior of the community, will be considered variable.

As an indication of the limiting effect of the medium on the community, we can report the mean value $\bar{\lambda}$*, while we can use the mean value $\bar{y}$ of the mortality vector $y=(y_\alpha)$ due to extrabiocenotic causes (behavior of the environment) as an indicator of the intensity of the action of death-causing factors of the environment on the community. The set of vectors y and λ, with nonnegative components, not exceeding unity, with fixed values of $\bar{y}$ and $\bar{\lambda}$, will be represented by $W_{\bar{y}}$ and $W_{\bar{\lambda}}$. Furthermore, additional conditions are placed on vector λ, related to equation (2.2). Therefore, the set $W_{\dot{\bar{y}}}$ of its possible values is included in the set $W_{\bar{y}}(W_{\dot{\bar{y}}}\ W_{\bar{y}})$. We note that analogous limitations on the vector $\mu=(\mu_\alpha)$ in our case extend only to the fixed vector x and do not effect the vector y.

Empirical analysis of succession processes in a community reveals a tendency toward S-shaped growth of its summary biomass right up to the limiting climax value, limited by the steady conditions of the environment. This tendency, accompanied by fluctuations in the biomass of the individual components, is considered by Yu. Odum as a strategy of the community (Odum, 1975, p. 345).

Let us formalize these general ecologic concepts within the framework of the model for quantitative analysis which we have studied.

Grouping populations within components, we can achieve relatively small differences in mean densities β_α of the biomasses of α-individuals. If this, for any reason, cannot be done, then we must limit ourselves to analysis of only the higher trophic levels of multicomponent communities, for which β_α is not divided into orders. The assumptions we have made allow us to extend the tendency toward growth of the summary (or mean) biomass of the community to the mean population density $\bar{\rho}$, which is proportional to the mean probability $\bar{p}$ (see above). Thus, we can consider the following function, monotonically increasing $\bar{p}$, to be the "goal functional" of the community:

$$M = M(\lambda,\mu) = \bar{p}/\bar{\lambda}(1 - \alpha\bar{p}) = \frac{1}{\bar{\lambda}\alpha} \sum_{\alpha=1}^{\alpha} \lambda_\alpha/\mu_\alpha = \frac{1}{\bar{\lambda}} \left(\frac{\bar{\lambda}}{\mu}\right). \qquad (2.15)$$

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*In what follows, the averaging operator $\bar{x}$ represents $x= \frac{1}{\alpha} \sum_{\alpha=1}^{\alpha} x_\alpha$ see (2.13) .

The strategy of the community is to maximize the value of M ($\max_{\lambda} M$) with respect to $\lambda \in W'_{\bar{y}}$.

There is no basis for advance determination of the degree of indifference of the environment to a community, therefore, in order to guarantee the following results and conclusions, we must expect the "worst" action of the environment on the community y, i.e., that action which would minimize M($\min_y M$) with respect to $y \in W'_{\bar{y}}$. Thus, we must analyze the expressions:

$$\min_{y \in W_{\bar{y}}} \; \max_{\lambda \in W'_{\bar{\lambda}}} M\,[\lambda,\ \mu(x,\ y)] \leqslant \min_{y \in W_{\bar{y}}} \; \max_{\lambda \in W_{\bar{\lambda}}} M[\lambda,\ \mu(x,y)], \tag{2.16}$$

$$\max_{\lambda \in W'_{\bar{\lambda}}} \; \min_{y \in W_{\bar{y}}} M[\lambda,\ \mu(x,\ y)] \leqslant \max_{\lambda \in W_{\bar{\lambda}}} \; \min_{y \in W_{\bar{y}}} M[\lambda,\ \mu(x,y)]. \tag{2.17}$$

We note that whereas in function M as we expand the set of values of $W'_{\bar{y}}$ to $W_{\bar{y}}$ no new maxima appear with respect to λ, relationships (2.16) and (2.17) are converted to equations. This occurs for all cases of practical interest.

First of all, let us produce general estimates using the equation $M = M(\lambda,\ \mu)$, by varying λ and μ. It can be shown, by using the Bunyakovskiy equation, that:

$$\max_{\lambda} \min_{\mu} M(\lambda,\ \mu) = \min_{\mu} \max_{\lambda} M(\lambda,\ \mu) = M(\tilde{\bar{\lambda}}e,\ \bar{\mu}e) = \frac{1}{\bar{\mu}}, \tag{2.18}$$

where $e = (\overbrace{1, \ldots, 1}^{\alpha})$. However, the requirement for constancy of $\mu_{\alpha} = \mu(x_{\alpha},\ y_{\alpha}) = \bar{\mu}$ is unrealistic, if we consider the variability of the vectors of x and y.

Consideration of the conditional extremes with respect to λ and y involves great analytic difficulties and leads to the following results. The minimax equation (2.16) leads to a degenerate case of a community (some of the components of vector λ vanish). The maximin equation (2.17) leads to the following important results.

Let us represent $M\{\lambda,\ \mu(x,\ y)\} = M_x(\lambda,\ y)$ and

$$\begin{aligned} &\min(1-\bar{y},\ 1-\bar{y}) = M_x(\lambda_{\bar{y}},\ y_{\bar{y}},\ \lambda_{\bar{y}}) = \\ &\max_{\lambda \in W_{\bar{\lambda}}} M_x(\lambda,\ y_{\bar{y}},\ \lambda) = \max_{\lambda \in W_{\bar{\lambda}}} \; \min_{y \in W_{\bar{y}}} M_x(\lambda,\ y), \end{aligned} \tag{2.19}$$

where $y_{\bar{y}}, \lambda$ is the extreme value of $\underline{y}$ with fixed $\bar{y}$ and λ, while $\lambda_{\bar{y}}$ is the extreme value of λ with fixed $\bar{y}$ and $\bar{\lambda}$.

Of primary significance is the function:

$$m(1 - \bar{y}_1, 1 - \bar{y}_2) = M_x(\lambda_{\bar{y}_2}, y_{\bar{y}_1}, \lambda_{\bar{y}_2}),$$

obtained by replacing in $M_x(\lambda, y_{\bar{y}_1}, \lambda)$the extreme value of $\lambda = \lambda_{\bar{y}_1}$ with the extreme value of $\lambda = \lambda_{\bar{y}_2}$ $(\bar{y}_2 \neq \bar{y}_1)$. This function, as in the theory of statistical selection among hypotheses (Basharinov, Fleishman, 1962) will be called the operative characteristic. Using the method of multipliers, we find its expression:

$$m(\bar{z}_1, \bar{z}_2) = \upsilon(\bar{x}_2) + \gamma(\bar{x}_1, \bar{x}_2) \sqrt{\nu'(\bar{z}_1)\ \nu'(\bar{z}_2)}\ (\bar{z}_1 - \bar{z}_2), \qquad (2.20)$$

where the function $v(\bar{z})$ is the solution of the transcendental equation:

$$\bar{z} = \overline{[(\frac{1 - x}{1 - 2x})^{-1} + \nu^{-1}]^{-1}} \qquad (2.21)$$

while the function $\lambda(\bar{z}_1, \bar{z}_2)$ is:

$$\gamma = \gamma(\bar{z}_1, \bar{z}_2) = \sqrt{\frac{\nu'(\bar{z}_2)}{\nu'(\bar{z}_1)}} \Big/ \sqrt{\frac{\nu'_0(\bar{z}_2)}{\nu'(\bar{z}_1)}}, \qquad (2.22)$$

while the expression $v_0(\bar{z})$ is defined as follows.

Equation (2.21) has a solution if the structure of the community is "linear," in which case:

$$\frac{1 - 2x_\alpha}{1 - x_\alpha} = C + \Delta \frac{\alpha - 1}{\alpha - 1} \ (\alpha = 1, \alpha),$$

where $C = \frac{1-2x_1}{1-x_1}$ and the quantity $\Delta = \frac{x_1-x_a}{(1-x_1)(1-x_a)}$ characterizes the "standardized difference" of mortality of components of the community.

for large values of a, we can obtain an explicit expresion for $v(\bar{z})$:

$$\nu(\bar{z}) = \nu\Delta\ (\bar{z}) = [g\Delta^{-1}(\bar{z}) - g\Delta^{-1}((\frac{\overline{1 - x}}{1 - 2x}))]^{-1}, \qquad (2.23)$$

where

$$g\Delta(\bar{z}) = (e^{\Delta\bar{z}} - 1)/\Delta, \qquad (2.24)$$

and, since $g_0(\bar{z}) = \bar{z}$, then:

$$\nu_0(\bar{z}) = [(\bar{z})^{-1} - ((\frac{\overline{1 - x}}{1 - 2x}))^{-1}]^{-1}. \qquad (2.25)$$

It is convenient for the remainder of our presentation to introduce the following function:

$$\delta = \delta(\bar{z}_1, \bar{z}_2) = \frac{\nu(\bar{z}_1) - \nu(\bar{z}_2)}{\sqrt{\nu'\ (\bar{z}_1)\ \nu'\ (\bar{z}_2)}\ (\bar{z}_1 - \bar{z}_2)} . \qquad (2.26)$$

It can be shown that in the linear case, when $v(\bar{z}) = v_\Delta(\bar{z})$ the corresponding expressions $\lambda = \lambda_\Delta$ and $\delta = \delta_\Delta$ become:

$$\gamma\Delta = \frac{(1 + \Delta/C) - e^{\Delta\bar{z}_1}}{(1 + \Delta/C) - e^{\Delta\bar{z}_2}}\ \frac{\ln\ (1 + \Delta/C) - \Delta\bar{z}_2}{\ln\ (1 + \Delta/C) - \Delta\bar{z}_1} \cdot e^{-\Delta(\bar{z}_1-\bar{z}_2)'2} \qquad (2.27)$$

and

$$\delta_\Delta = [e^{\Delta(\bar{z}_1-\bar{z}_2)'2} - e^{-\Delta(\bar{z}_1-\bar{z}_2)'2}]/\Delta(z_1-z_2) = \frac{Sh[\Delta(\bar{z}_1-\bar{z}_2)/2]}{\Delta(\bar{z}_1-\bar{z}_2)/2} . \qquad (2.28)$$

In general, the extreme values of the conditional probability $y_{\bar{y}_1,\lambda} = (y^0_\alpha)$, $y_{\bar{y}_1,\lambda\bar{y}_2} = (y^\star_\alpha)$, $\lambda_{\bar{y}_2} = (\lambda^0_\alpha)$ and the absolute probability $p = (p^0_\alpha)$ are:

$$\begin{aligned} y^0_\alpha &= \bar y_1 - (X_\alpha - \bar X) + (\bar X + \bar y_1)\left[\frac{(1 + X_\alpha)\sqrt{\lambda_\alpha}}{(1 + \bar X)\sqrt{\bar\lambda}} - 1\right], \\ y^*_\alpha &= \bar y_1 - (X_\alpha - \bar X) + \frac{\bar X + \bar y_1}{\bar X + \bar y_2}\left[\frac{(1 + X_\alpha)^2}{1 + X_\alpha + v(\bar z_2)} - (\bar X + \bar y_2)\right], \\ \lambda^0_\alpha &= \bar\lambda\left(\frac{1 + X_\alpha}{1 + X_\alpha + v(\bar z_2)}\right)^2 \Big/ \overline{\left(\frac{1 + X}{1 + X + v(\bar z_2)}\right)^2}, \\ p^0_\alpha &= \bar p \lambda^0_\alpha / \bar\lambda, \end{aligned} \tag{2.29}$$

where:

$$X_\alpha = \frac{x_\alpha}{1 - 2x_\alpha} \quad (\alpha = \overline{1, \alpha}).$$

Their analysis, in contrast to the minimax case, produces no disagreement with general ecologic concepts. For example, dominance (nonuniformity of density ρ_α or probability ρ^0_α) is a result of nonuniformity of distribution of components of vector λ which, in turn, is a result of heterogeneity of the structured vector $x = (x_\alpha)$. If this vector is homogeneous ($x_\alpha \equiv \bar x$, $\gamma_0 = \delta_0 = 1$), all characteristics of the community become homogeneous ($y^0_\alpha \equiv \bar y$, $\lambda^0_\alpha \equiv \bar\lambda$, $p^0_\alpha \equiv \bar p$). In this case, there are no degenerate values of the components of the vector $\lambda = (\lambda_\alpha)$. Thus, the model in question provides no basis for rejecting maximin optimization of the community. The problem of the sequence of occupation of the conditional extremes $\max_\lambda \min_y M$ or $\min_y \max_\lambda M$ is of basic significance. It is related to the fact that the first case corresponds to the homeostatic principle of the "stimulus-reaction" decision, while the second case corresponds to a more complex "reaction-stimulus" decision, involving prospective activation. Here, in contrast to the case of populations, at the level of qualitative analysis of the model, without using empirical material, we must give preference to the hypothesis that the community follows the principle of "stimulus-reaction." This indicates some regression of the biocenosis in comparison to populations, in which pre-adaptation-type "reaction-stimulus" decisions are quite likely (Fleishman, 1971). These relationships are of more than qualitative interest. As will be shown below, they can be used for quantitative analysis of the adaptation cycle of a community, related to its peak stability (Odum, 1975, p. 347).

In the environment, if there are no anthropogenic factors present, great deviations are improbable, i.e., large values of $\bar y \gg \bar x$ are improbable, and therefore occur rarely (are separated by long mean intervals of time). During these time intervals, the community succeeds in adjusting to a state close to the steady state. This means that we are justified in analyzing only the steady state of the goal functional (2.15). However, the concept of the norm and the depressed state of a community cannot be related to any specific value of harmful effects of the environment $\bar y$. Furthermore, any such effects, if they have sufficiently long-term stability, after the community adapts to them ($\lambda = \lambda_{\bar y}$), can be considered normal, and the community itself can be considered to be in the normal state. This might be called adaptive accumulation of the harmful environmental effects by the community. In the model we are analyzing, this corresponds to the following formal identity:

$$\mu(x_\alpha, y_\alpha) \equiv \mu\{\mu(x_\alpha, y_\alpha), 0\}.$$

Let us perform the following mental experiment, utilizing the operational characteristic. Suppose a long-term adaptation, reflected by vector $\lambda_{\bar{y}}$, places the community in the normal state, which corresponds, with assigned structure x, to the value of the operational characteristic m(1, 1). This is its ideal value. Actually, there are always certain weak perturbing environmental effects $\bar{y} \neq 0$, but in the normal state $\bar{y} \ll \bar{x}$ we can ignore them, since in this case $m(1 - \bar{y}, 1 - \bar{y}) \simeq m(1, 1)$. Suppose the environment suddenly applies a strong harmful $\bar{y} > \bar{x}$ to the community. In the worst version of this case, the corresponding value of the operational characteristic will be $m(\bar{z}, 1)$, where $\bar{z} = 1 - y < 1 - \bar{x}$. Immediately after this, we will consider the community to be in a depressed state. Then, after a certain, rather long, time interval has passed, due to adaptation, reflected by the vector $\lambda = \lambda_{\bar{y}}$, the first adapted rise of the community occurs (increase in mean population of individuals). This corresponds to the value of the operational characteristic $m(\bar{z}, \bar{z})$. Suppose now that the harmful factor of intensity $\bar{y} = 1 - \bar{z}$ is relieved. Immediately after this, a passive rise of the biocenosis occurs (increase in mean population of its individuals). This corresponds to the value of the operative characteristic $m(1, \bar{z})$. However, this does not exhaust the capabilities of the community, since over a sufficient period of time, readapting along vector λ from the value $\lambda_{\bar{y}}$ to the value λ_0, it once more returns to its previous state, defined by m(1, 1), performing a second adaptive rise. This sequence of effects and adaptations will be called the adaptation cycle. In accordance with ecologic concepts, the corresponding values of the operative characteristic (2.20) satisfy the equations:

$$m(1, 1) > m(1, \bar{z}) \geqslant m(\bar{z}, \bar{z}) \geqslant m(\bar{z}, 1). \qquad (2.30)$$

Their relative difference will be called the first and second adaptive and passive rises and represented by Δ_{a1}, Δ_{a2} and Δ_n, respectively. Their ratios to the maximum value m(1, 1) are represented by $\mu_2 > \mu_3 > \mu_4$, respectively.

The sum of first values is 1, and the values are expressed through the parameters γ and δ as follows:

$$\begin{aligned}
\Delta_{a1} &= \frac{m(\bar{z}, \bar{z}) - m(\bar{z}, 1)}{m(1, 1) - m(\bar{z}, 1)} = 1 - \delta\gamma, \\
\Delta_n &= \frac{m(1, \bar{z}) - m(\bar{z}, \bar{z})}{m(1, 1) - m(\bar{z}, 1)} = \gamma^2, \\
\Delta_{a2} &= 1 - \Delta_{a1} - \Delta_n.
\end{aligned} \qquad (2.31)$$

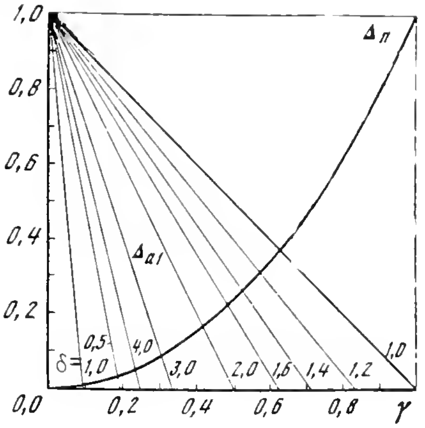


Fig. 9. Adaptive (Δ_{a1} and Δ_{a2}) and passive (Δ_n) rises as functions of coefficients of nonlinearity (δ) and heterogeneity (γ).

Furthermore, the following estimates are valid:

$$\mu_3 \geqslant \Delta_{a1}, \quad \mu_2 \geqslant \Delta_{a1} + \Delta_n. \qquad (2.31')$$

Therefore, it is sufficient to calculate the first two values of Δ_{a1} and Δ_n, in order to determine their weight. The nomogram which this requires is presented in Fig. 9.

It is important to be able to estimate the mean probabilities $\bar{p}$ [see (2.15)], corresponding to values of the operative characteristic of the adaptive cycle $\bar{p}_1 \geqslant \bar{p}_2 \geqslant \bar{p}_3 \geqslant \bar{p}_4$. Their ratios to $\bar{p}_1$ $\pi_2 = \dfrac{\bar{p}_2}{\bar{p}_1} \geqslant \pi_3 = \dfrac{\bar{p}_3}{\bar{p}_1} \geqslant \pi_4 = \dfrac{\bar{p}_4}{\bar{p}_1}$ are expressed through the corresponding values of μ_2, μ_3 and μ_4 as follows:

$$\pi_i = \frac{\mu_i}{1-\alpha\bar{p}_1(1-\mu_i)} \geqslant \mu_i \quad (i = 2,\ 3,\ 4). \qquad (2.32)$$

Thus, for full calculation of all of the parameters of interest to us, it is sufficient to be able to calculate the parameters δ and γ, which, in the general case, requires solution of the cumbersome transcendental equation (2.21). Also, the linear case $v(\bar{z}) = v_\Delta(\bar{z})$ fits practically completely in the order of accuracy of the initial experimental data on the values of x^*_α ($\alpha = \overline{1, a}$) . Actually, if we number the components of the community in order of decreasing mortality of their individuals $\bar{x}_1 \geqslant \bar{x}_2 \geqslant \ldots \geqslant \bar{x}_\alpha \geqslant \ldots \geqslant \bar{x}_\alpha$, and then, using the method of least squares, straighten their function

$$\frac{1 - 2x^*_\alpha}{1 - x^*_\alpha} \approx c^* + \Delta^* \frac{\alpha - 1}{a - 1},$$

the quantities C* and Δ* can serve as experimental estimates of the theoretical parameters

$$C = \frac{1 - 2x_1}{1 - x_1} \text{ and } \Delta = \frac{x_1 - x_a}{(1 - x_1)(1 - x_a)} .$$

For numerical calculations, it is convenient to analyze the asymptotic case of small values of Δ, when the expressions (2.27) and (2.28) are simplified:

$$\gamma\Delta \approx \frac{\frac{1}{c} - \bar{z}_1 - \frac{\Delta\bar{z}_1^2}{2}}{\frac{1}{c} - \bar{z}_2 - \frac{\Delta\bar{z}_1^2}{2}} \, \frac{\frac{1}{c} - \bar{z}_2 - \frac{\Delta}{2c^2}}{\frac{1}{c} - \bar{z}_1 - \frac{\Delta}{2c^2}} \left(1 - \frac{\Delta(\bar{z}_1 - \bar{z}_2)}{2} + \frac{\Delta^2(\bar{z}_1 - \bar{z}_2)^2}{24}\right), \quad (2.33)$$

$$\delta\Delta \approx 1 + \frac{\Delta^2(\bar{z}_1 - \bar{z}_2)^2}{24} . \quad (2.34)$$

To estimate the mean probabilities of α-individuals of a community $\bar{p}$, we must estimate the mean birth rate $\bar{\lambda}$ of its individuals, limited to a great extent by the trophic nature of the area of distribution. These estimates represent a special problem in trophodynamics. The importance of the equations presented above for the relative indices Δ and π consists in that they can be calculated without knowing the values of $\bar{\lambda}$, before they are determined. Let us analyze a numerical example of the use of these equations.

Suppose, within an a-component community (a = 10) with a mean probability of α-individuals within it $\bar{p}_1 = 0.01$ and assigned parameters C = 0.1 and Δ = 0.15, there is a commercial population of interest to us (component α) and we would like to exploit it annually (time step of model one year) so that the corresponding parameter $y_\alpha = 0.4$, while leaving the other components alone ($\bar{y} = y_\alpha = 0.4 = 1 - \bar{z}$). What, in this case, is the maximum possible value of the relative mean probability of α-individuals of the community $\pi_2 = \bar{p}_2/\bar{p}_1$, and what is the possible increase in π_4 to the value $\pi_3 = \bar{p}_3/\bar{p}_1$, after some rather long time of readaptation of the community to the new conditions of stable (with characteristic $\bar{y}$) exploitation?

By definition, we have

$$\pi_3 \geqslant 0.5 \text{ and } \pi_2 \geqslant 0.75,$$

the quantities 0.5 and 0.75 were defined as follows: first, using C = 0.1 and Δ = 0.15 and the equations (2.33) and 2.34), we found the values of λ = 0.5 and δ = 1, then, using them and Fig. 9, we determined the values of $\Delta_{a1} = 0.5$ and $\Delta_n = 0.25$; then using them and equations (2.31'), we found the values of the estimates $\mu_3 \geqslant 0.5$ and $\mu_2 \geqslant 0.75$ and then, finally, using them, we found the desired values of the estimates π_3 and π_2 (see (2.32)).

Obviously, similar estimates can be performed to predict the results of other strong effects, related to pollution, catastrophes and other harmful influences on a community.

2.3 Static Model of a Community Considering Aggregation.

The construction of a dynamic stochastic model considering aggregation is quite difficult. Therefore, let us analyze a static case of this model or a 2-component community (a=2) consisting of a predator and its prey, referring to the aggregations of the predator as schools, of the prey as spots.

A set consisting of N objects will be referred to as a N-set. In a single biotope with the volume V_q(q = 2 for area, q = 3 for volume), we analyze the N-field of food particles and the M-accumulation of individual predators. The aggregation of food particles is determined by the ν n-spots ($N = \nu.n$), the aggregation of the latter by the μ m-schools. Furthermore, the former aggregation can be described by the two parameters r_n and 1, where r_n is the radius of a sphere equal in volume to n-spot or a half-side of an equivalent cube, while 1 is the distance between their centers. With the distribution of n-spots stable in the probabilistic sense, r_n and 1 act as constant means. From the standpoint of the m-school, the value of r_n is replaced by the quantity $r = r_n + r_m$, where r_m is the distance from the edge of n-spot to the point where m-school will reliably detect n-spot (this quantity has a precise statistical sense.

It can be shown (Fleishman, 1974), that the mean specific ration R_m of individuals within m-school is

$$R_m = \left(\frac{\rho_q y_m^{q-1}}{m} - z\right)w \text{ particles per day} \qquad (2.35)$$

where y_m(meter) is

$$y_m = \min(r,\ 1) = \begin{cases} 1, \text{ if } 1 < r \text{ (directed catching)} \\ r, \text{ if } r < 1 \text{ (blind search);} \end{cases} \qquad (2.36)$$

z (in particles/meter) is the energy cost expressed in individuals, equivalent to the loss of z food particles in one meter of travel path, w (meter/day) is the mean speed of movement of m-school.

The expression R_m will now be analyzed given the constant value:

$$\rho_q = \frac{N}{V_q} \ \left(\frac{\text{particles}}{\text{meters}^q}\right) = \text{const}$$

Of the mean construction of food and the variable aggregation of food, defined by the parameter 1 or $\nu = V_q/1^q$.

The double representation (2.36) of the value of y_m results from the two possible modes of hunting of an active predator seeking passive prey (we shall not consider the case of a passive filter-feeder, which simply waits for food to "swim up" to it). We are concerned with the mode of directed ("visual") search ($r > 1$), in which n-spots are always located within the field of detection of m-school, and the school sequentially consumes the spots, as well as the mode of blind search, in which m-school finds n-spots by randomly encountering them ($1 > r$), or more accurately, by randomly approaching them until the radius of detection r_m is reached.

The basic formula (2.35) and its various interpretations have been used for analysis of materials of the 17th cruise of the research vessel AKADEMIK KURCHATOV. On this cruise, a visual count was made of the number of flying fish and schools of flying fish (groups of at least ten fish) in a section along the equator in the eastern Pacific, and the time intervals between sightings were recorded. Processing of a portion of these materials (ignoring the individual fish) produced the data of Fig. 10. These included λ(km)--the mean distance between sightings, m--the mean number of fish in each school, and $\rho(\mathrm{km}^{-2})$--the density of the number of fish. This last quantity is calculated from the first two:

$$\rho = m/\lambda^2. \tag{2.37}$$

All means were calculated for a single day. The schools of flying fish were encountered only west of 120°W, with a clear maximum in their density at about 135°W. It is probable that this maximum is explained by an increase in the concentration (mg/meter^3) of zooplankton near the surface, the food of the flying fish. However, data kindly provided to us by A. G. Timonin clearly show that the biomass of zooplankton in the upper 100 meter and 10 meter layers is practically constant between 120° and 155°W (β = 75 mg/meter^3), while the increase in the value of β east of 120°W is located in a zone where the water temperatures are too low for flying fish (< 21°C). Thus, we must assume that the abundance of flying fish also depends on the aggregation of zooplankton for a fixed density $\rho_3 = \beta/b(\mathrm{meter}^{-3})$, where ρ_3 is the number of zooplankters per meter^3, b is the mean biomass of one zooplankter.

To explain this effect, we applied the theoretical equation (2.35):

$$R_m = \left(\frac{\rho_3 y^2}{m} - z\right)w, \tag{2.38}$$

Where $R_m(\mathrm{day}^{-1})$ is the mean specific ration of flying fish in a school of m fish, $y = \min(1, r)$, 1(meter) is the mean distance between zooplankton spots, $r = r_m + r_n$ (m), r_m is the mean radius of detection of a spot by a school, $r_n = \sqrt{\rho_3/\rho_{3n}}\,1$ is the mean radius of a spot ($\rho_{3n} > \rho_3$ represents increased density of a spot), $z(\mathrm{meter}^{-1})$ are the energy losses of the flying fish in "standard" zooplankters per meter of travel distance, w(meter/day) is the mean speed of the school.

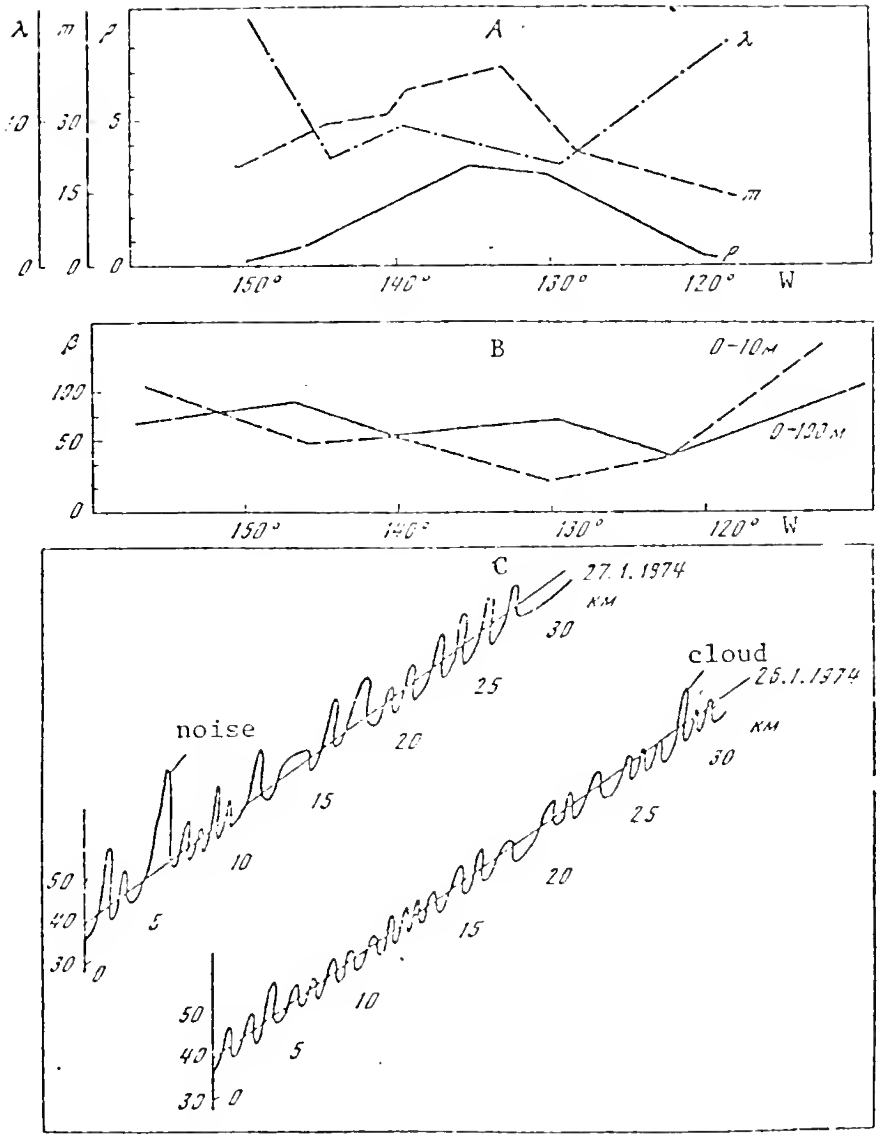


Fig. 10. Experimental data on the distribution of flying fish (A), zooplankton (B) and phytoplankton (C) in the region of the equator at 120-150°W. Explanation in text.

Since in the case in question all of the values in equation (2.38) are constant except for y and m, while the value of y is proportional to 1, it leads us to the following theoretical equation:

$$m = c1^2, \qquad (2.39)$$

Where c is a constant coefficient: for the case in question, c = 7. Therefore, together with m, according to equations (2.37) and (2.39), curve ρ becomes a theoretical function (a quadratic function) of parameter 1--the aggregation of the food.

Experimental comparison of these values was not performed, due to the difficulty of observing the aggregation of zooplankton. Therefore, we could judge the spottiness of the plankton only indirectly, on the basis of the spottiness of the distribution of phytoplankton. The spottiness of phytoplankton in the region of interest to us was measured by optical methods (based on the absorption of light by chlorophyll) in two sessions of approximately one hour each (these data were kindly provided to us by V. N. Pelevin). To estimate the number of spots, a threshold of 40 units, located in the moddle of the spread of both curves, was arbitrarily selected. Using this threshold, on the curve obtained on 26 January 1964, 23 excursions were noted, on the curve obtained on 27 January--16 excursions. Given the mean speed of the ship of 30 km/hr, the mean distances between spots of phytoplankton (1) was defined as 1.3 and 1.9 km, while the mean number of flying fish on these days (m) was 12 and 23. A numerical count shows good agreement of the values m and 1 obtained with the theoretical equation (2.39).

The value $c = m/1^2 \approx 7$ was defined for 26 January; for 27 January, the "theoretical" value of m was 25.3, which differs only slightly from the observed value (23). Thus, we can present the following theoretical equation for the density of predators, given constant density ρ_n = const of prey, as a function of the aggregation of the prey 1:

$$\rho = c(1/\lambda)^2$$

Where c is a constant related ρ_n, depending on the type of predator and prey, 1 and λ are the mean distances between schools of predators and spots of prey.

PART 2. HUMAN ACTIVITY AND THE BIOLOGY OF THE OCEAN

CHAPTER I. BIOLOGICAL RESOURCES OF THE OCEAN AND POSSIBILITIES FOR INCREASING THEM

1. Fishery Production of the World Ocean and Its Utilization.

(P. A. Moiseev)

In recent years, many nations of the world have shown increasing interest in the study and utilization of the biologic resources of the ocean. This has resulted primarily from an increasing shortage of animal protein--the most important and irreplaceable component part of the diet of the rapidly growing population of the world. Even today, with the population of the planet approaching 4 billion people, more than one half of the world's people do not receive a sufficient quantity of animal protein, or even are simply starving. This is particularly true of the developing nations of Asia, Africa and Latin America (Table 1).

Table 1. Daily consumption of animal protein by the population of the earth (excluding the Socialist countries), expressed in % of the total population.

Consumption of Animal Protein	1938	1960	1970
In Weight Units, g			
<15	59.0	60.7	62.0
15-30	18.9	19.8	20.7
>30	22.1	19.5	17.3
In Calories			
<2200	38.6	59.4	63.0
2200-2700	30.8	19.0	17.0
>2700	30.6	21.6	20.0

Specialists in the area of nutrition believe that the daily consumption of 30 g of animal protein is sufficient for good nutrition, while consumption of less than 15 g per day is insufficient and dangerous for health. Thus, an ever increasing fraction of the world's population, already more than half, is suffering from chronic malnutrition.

We know that 1 ha of land, given modern methods of cultivation, can feed 7 people. At present, some 1.4 billion ha of the earth's surface (approximately 10% of the continental surface) is under cultivation, so that the fruits of agriculture, given intelligent use and distribution, could feed 10 billion people. If agriculture were improved and planted areas expanded, these capabilities could be still further increased. However, agricultural production, and particularly animal husbandry, require great efforts and capital investments, which are amortized over a long period of time. Therefore, the self-renewing biologic resources of the World Ocean have, in recent decades, become an important source of nutrition, animal feed, and medical and engineering products.

Year	1800	1850	1900	1960	1970	1975
Population of the world in millions	800	1000	1550	3000	3635	4000
Catch per person, kg	1.5	2.0	2.6	13.3	19.2	16.9

The volume of the total worldwide catch from the ocean in the early twentieth century was around 4 million tons, i.e., 2.6 kg per inhabitant of the earth. The rapid increase in the catch in recent decades has meant that by 1960, some 40 million tons were taken from the sea (13.3 kg per person), in 1970-1975--65-70 million tons (17-19 kg per person). At present, products obtained from the seas and oceans account for 15% of the balance of food proteins, significantly less than the fraction accounted for by milk and meat. However, a comparison of the total volume of food obtained by man from the sea and from the land indicates that the "fields of the sea" provide a more than modest harvest. About 3% of the surface of the earth--the area of cultivated land--provides almost 99% of the food eaten by man, whereas the other 71% of the earth's surface, covered by the seas and oceans, provides man with slightly over 1% of his food.

According to modern best estimates, each year, some 300-320 million t of fish and large invertebrates are produced in the ocean, of which about 90 million t could be caught by man. Thus, there are genuine possibilities for significantly increasing the catch, but, at the same time, the demands of mankind are such that by the year 2000 it would be desirable to obtain as much as 140-150 million t of fish and related products--that is, twice the present level.

What are the potential capabilities of the World Ocean as a source of food, to what extent and by what methods can the harvest of the "blue fields" be increased, and what is the reason for the relatively low yield of food from the tremendous area of the World Ocean? These questions must be answered in order to provide an objective evaluation of the possible volume of commercial production of the ocean.

In recent decades, research vessels have made thousands of voyages to all regions of the World Ocean; hundreds of thousands of fishing ships are at work each day, catching fish down to depths as great as 2,000 m, at all distances from their bases, using the most modern equipment available for the detection and catching of commercial varieties of fish. As a result, an extensive fund of data has been accumulated concerning the topography of the bottom of the World Ocean, the oceanographic characteristics of its various regions, and the regularities of the processes which define the biologic productivity of the ocean. They allow us to form an approximate idea of the volume of commercial production formed each day in the World Ocean and the peculiarities of its distribution and reproduction.

1.1 Productive Regions of the Ocean.

The biologic productivity of the World Ocean and, in the final analysis, the volume and nature of its commercial production, depend to a great extent on the relief, hydrological and hydrochemical regimes, atmospheric processes, balance of nutrients, and on the peculiarities of the productivity of phytoplankton and zooplankton. We should emphasize a few facts which are of particular significance for an understanding of the peculiarities of the production and distribution of the biological resources of the World Ocean.

Only 7.4% of the area of the ocean is less than 200 m deep, only 11.4% is less than 1,000 m deep. Almost 77% of the area of the ocean is over 3,000 m deep (Table 2). If we consider that the most extensive shallow-water areas are located in the Arctic, with a great deal more in the Antarctic, we find that the total area of regions favorable for habitation by commercial benthic animals is about 30 million km^2--only 8% of the area of the ocean. However, it is the continental shelf and the waters of the peripheral regions of the ocean which are most productive and it is this area, 20% of the water area of the ocean, which acounts for some 90% of the present world catch. This uneven distribution of the catch is primarily a result of the fact that areas of high biologic productivity are to be found around the edges of the oceans.

It has been established in recent years that a significant quantity of fish, in accumulations dense enough to allow successful commercial fishing, may be formed in individual areas of the World Ocean far from the coast, near the slope or over elevated areas of the deep-sea floor (with depths as great as 2,000 m). This type of concentration results from the existence in these regions of an intensive upwelling of deep water, resulting in the creation of zones of increased biologic productivity. There is good reason to believe that commercial concentrations of fish will be found over some of these underwater elevations, with a total area of about $1.5 \cdot 10^6$ km^2.

The most productive zones, with the daily primary productivity of about 1.2 g C/m^2 and zooplankton biomass of over 100 mg/m^3, cover about 17% of the total area of the ocean. This is approximately the same level of productivity as that of continental ecosystems--forests and

Table 2. Area of primary parts of the floor of the World Ocean.

PORTION OF BOTTOM	DEPTH, m	OCEAN									
		WORLD		PACIFIC		ATLANTIC		INDIAN		ARCTIC	
		$km^2 \cdot 10^3$	%	$km^2 \cdot 10^3$	%	$km^2 \cdot 10^3$	%	$km^2 \cdot 10^3$	%	$km^2 \cdot 10^3$	%
Shelf	<200	26,661	7.4	9,377	5.3	9,213	9.9	3,171	4.2	4,900	37.4
Continental slope	200-3,000	57,417	15.9	24,478	13.7	16,093	17.3	10,410	13.9	6,436	49.1
Deep floor	>3,000	276,145	76.7	145,824	81.0	68,057	72.8	61,336	81.9	1.764	13.5
Total	—	360,223	100.0	179,679	100.0	93,363	100.0	74,917	100.0	13,100	100.0

pasture lands. Zones of low productivity, not exceeding the productivity of deserts, occupies some 63% of the area of the ocean. The 37% of the ocean occupied by productive regions accounts for over 70% of the primary production. The edible benthos is still more strongly restricted to the periphery of the ocean, 58% being concentrated at depths of less than 200 m and 90% at depths of less than 100 m.

According to approximate calculations, the total quantity of zooplankton accessible to animals of higher trophic levels, principally fish, is about 6-20 billion tons. The biomass of the benthos is relatively low, not over 2.5 billion tons within the limits of the commercial depths (down to 1,000 m), including about 1 billion tons of edible benthos.

The results of complex oceanographic and fishing-industry studies of the World Ocean, undertaken in recent years, have allowed us to direct the development of Soviet fishing primarily toward the utilization of the biologic resources of the ocean which, in combination with the construction of a large, modern fishing fleet, has allowed us to achieve a rapid increase in the total catch and significant improvement in the quality of fish products supplied to our population. At the present time, the sea and ocean fishing industry of the USSR provides over 90% of the total fish catch eaten in the nation, and it is assumed that this industry will continue to play a dominant role in Soviet fishing in the future (Table 3).

Table 3. USSR fish catch ($t \cdot 10^3$).

Catch	1930	1940	1950	1960	1970	1975
Total	1,283	1,509	1,654	3,511	7,775	10,300
In open seas	380	965	945	2,736	6,750	9,168
In internal waters	903	744	709	775	1,025	1,132

Thousands of Soviet fishing, transportation and processing ships, utilizing the stock of fish available in the World Ocean, achieved an increase of the fish catch of the USSR from 2.7 to $10.3 \cdot 10^6$ t in 1955-1975. During these years, some 55 million tons of seafood were caught. The Soviet catch today represents about 14% of the world's production of seafood.

The increase in the total catch of sea fish has occurred primarily on the continental shelf and in the upper portion of the continental slope, as well as peripheral oceanic regions, especially in the southern hemisphere, which is less extensively fished. At the same time, there has been a relative decrease in the significance of traditional species (herring, cod, plaice, sea perch, etc.), a decrease in the significance of the most important fishing regions of the northern hemisphere, an increase in the number of species, the reserves of which have been reduced by overfishing, a decrease in the success of fishing for most traditional species of fish, and an increase in the importance of fish with lower or unusual food value (anchovy, pollock, Arctic cod, capelin, horse mackerel, etc.). The experience of world fishing during recent decades has confirmed that the intensity of commercial utilization of many traditional species is near its limit, which, in some cases, has already caused overfishing, basic disruption of ecosystems and harmful changes in the genetic structure of populations. The time has come for commercial use of the biologic resources of the lower trophic levels and the most rapid possible development of methods for the control of the biologic processes in the ocean, in order to make the transition from the current hunting stage of fishing to a controlled fish economy with stable fish productivity.

The need for man to take an active part in the control of the biologic production processes, to change their directions and results in his own interest, is becoming obvious.

1.2 The Level of the Modern Catch.

The mean fish productivity of the World Ocean is relatively low: in 1967, with a total seafood catch of 60 million tons (including a correction factor for the catch not accounted for), the productivity, in terms of the entire surface of the World Ocean, was only 167 kg/km^2 (Moiseyev, 1969). In 1970-1975, the total catch (including the same correction factor) approached 70 million tons, averaging 190 kg/km^2. In the most productive regions, the catch amounts to 0.06-0.07% of primary production, which is approximately the level achieved in the highly productive and intensively fished Caspian Sea (0.1%). Special calculations have allowed us to produce an approximate estimate of the potential level of fish production of traditional species in the World Ocean--about 90 million tons (Moiseyev, 1969). Thus, the current catch of fish and large invertebrates is approaching the limit. The world catch of fish and other seafood (excluding whales) is presented below (in millions of tons).

1850	1900	1913	1938	1950	1960	1965	1970	1971	1972	1973	1974	1975
1.5-2.0	4.0	9.5	10.0	21.0	21.1	40.0	71.0	70.9	66.2	66.8	70.5	69.7

What is the current level of human utilization of the fish productivity of the ocean?

Of the total volume of the world catch from the ocean (including whales), the overwhelming majority--90% in 1974--consists of fish, followed by invertebrates, then aquatic plants in third place and, finally, whales in fourth place (Table 4).

Most of these objects (about 90%) are retrieved from the seas and oceans. Over the postwar period, almost the entire increase in the world catch had resulted from further utilization of oceanic biologic resources. Since 1950, when the prewar level of the world fish catch was reached, through 1970, the catch of sea fish has increased by 35.5 million tons, of fresh-water fish--by only 6.0 million tons. After 1970, the total catch of sea fish significantly decreased (by 5.5 million tons by 1973) as a result of the catastrophic drop in the population of the peruvian anchovy, while the catch of fresh-water fish remained almost the same.

At the present time, inhabitants of the pelagic zone dominate commercial fishing (Table 5).

The catch of pelagic fish during the postwar period has increased by 27.5 million tons, to a great extent due to the Peruvian anchovy catch, to the point that it represents 70% of the total catch; the catch of benthic fish has increased by only 10.5 million tons. Doubtless, this process is related to some extent to the opening of new regions and methods to fishing, as a result of extensive research operations, as well as the improvement of sonar devices for finding schools of fish and fishing techniques. However, the successful development of pelagic fishing has resulted primarily from the dominance of the population of pelagic fish over that of the benthic inhabitants of the sea (Table 6).

Most (75%) of the catch consists of fish which feed on zooplankton and phytoplankton, 20% consists of predatory fish, predominantly small predators, while a very small fraction--4%--consists of fish feeding on the benthos. Planktonophages include the most numerous commercial fish: herring, anchovies, sauries, Scombridae, Carangidae, Scorpaenidae, etc. The benthophages include the Pleuronectidae, Cottidae, etc. The large predators include the sharks, tunas and swordfish, while smaller predators include the small tunas and many other fish.

In recent years, commercial fishing of pelagic fish has been developed primarily with a reduction in the catch of the most valuable inhabitants of the benthic waters, from the standpoint of food (cod, plaice, sea perch, etc.) as a result of a reduction in their population due to intensive fishing. The weight relationship (in %) of the catch of planktonophagous fish, predators, benthophages and euryphages (based on data from 1973) is as follows: 75:20:4:1.

Predatory fish feed primarily on planktonophagous pelagic fish, and, to a much lesser extent, benthophages. If we assume the feeding

Table 4. Structure of the world catch of objects from the sea (in millions of tons).

Items	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Total	54.92	58.55	61.69	64.89	63.69	71.02	71.14	66.42	66.80	70.50
Fish	48.17	52.11	54.92	57.93	57.02	64.02	64.26	59.25	59.48	62.99
Fresh-water and transient	8.55	9.12	8.95	9.27	9.99	11.22	11.82	12.17	12.48	12.40
Salt-water	39.62	42.99	45.97	48.66	47.23	52.80	52.44	47.08	47.00	50.59
Invertebrates and plants	5.05	5.12	5.51	5.94	5.62	5.97	5.93	6.39	6.60	6.75
Whales	1.70	1.32	1.26	1.02	1.05	1.03	0.95	0.78	0.72	0.70

Table 5. Composition of the world catch of fish by regions (%).

Items	1938	1948	1959	1965	1973
Pelagic Fish	60.0	56.8	63.1	67.8	69.0
Epipelagic fish open ocean	5.5	4.9	10.2	6.6	5.0
Neritic regions	54.5	51.9	52.9	61.2	64.0
Benthic Fish	40.0	43.2	36.9	32.2	31.0
Shelf	37.6	39.4	32.5	27.3	26.0
Slope	2.4	3.8	4.4	4.9	5.0
Total	100.0	100.0	100.0	100.0	100.0
Catch, $t \cdot 10^3$	16,400	15,470	24,880	39.620	46,810

Table 6. Catch of marine fish with various feeding habits.

	1940		1950		1960		1973	
Fish	$t \cdot 10^6$	%	$t \cdot 10^6$	%	$t \cdot 10^6$	%	$t \cdot 10^6$	%
Planktonophages	8.97	59	8.71	57	18.10	62	35.11	75
Phytoplanktonophages	0.32	4	0.60	7	6.12	34	8.92	19
Zooplanktonophages	8.65	96	8.11	93	11.98	66	26.19	56
Predators	4.70	31	5.13	34	8.49	29	9.40	20
Benthophages	1.15	8	1.04	7	2.24	8	1.87	4
Euryphages	0.29	2	0.36	2	0.38	1	0.48	1
Total	15.11	100	15.24	100	29.21	100	46.86	100

coefficient to be 7-8, we find that they consume approximately 80 to 90 million tons of planktonophages and about 10 million tons of benthophages. Thus, the total volume of planktonophagous fish removed each year by fishing and by the inroads of predators amounts to 120-130 million tons, the total quantity of benthophages lost in these two ways is about 12 million tons.

The relationship of the production of zooplankton and benthos available for utilization by fish and other larger animals within the limits of the peripheral zones of the ocean is about 15:1 (zooplankton 15 billion tons, benthos 1 billion tons). The catch of zooplanktonophages (including 2 million tons of whales and 1 million tons of squid) is also at present approximately 15 times greater than the catch of benthophages. It seems likely that the intensity of fishing of demersal fish (benthophages) has reached its limit or is close to it, but there is some possibility for an increase in the catch of planktonophages, by increasing the catch of the inhabitants of the pelagic zone of the open ocean, where approximately the same quantity (15-20 billion tons) of zooplankton is produced as in the peripheral zones. Analysis of the volume and composition of the world fish catch confirms this conclusion.

In spite of the great variety of species of fish which are utilized by the fishing industry, the fate of world fishing is determined by an extremely limited number of families and species of fish, which have large populations. Representatives of seven families--the inhabitants of the continental shelf and the neritic areas of the ocean (the Engraulidae, Clupeidae, Gadidae, Carangidae, Thunnidae, Pleuronectidae and Scombridae) provide about 70% of the world catch of sea fish (Table 7).

The most numerous species, such as the Peruvian anchovy, the pollock, Atlantic cod an oceanic herring, the Caspian hake, the capelin and a few species of sardines, yield about 25 million tons in certain years, which is the majority of the catch of sea fish. The Peruvian anchovy alone in some years has yielded over 18% of the world catch, and about 25% of the catch of sea fish.

It is characteristic that in recent years, the catch of many important commercial fish, in spite of more intensive fishing, has significantly decreased. Many traditional fishes, which have long been greatly used as commercial fish, specifically the ocean herring, Atlantic cod, plaice, and Peruvian anchovy, have shown clear signs of depression of their reserves, which has directly influenced the volume of fishing and led to a reduction in the total volume of the world catch.

Before 1972, the anchovies held first place in the world fish catch, their 1970 yield reaching 14.6 million t (Table 8). In 1973, the anchovy catch dropped to 4.0 million t.

Most of the anchovy catch is represented by the Peruvian anchovy. In recent years, the catch of cape anchovy and northern Pacific anchovy

Table 7. Distribution of the world catch of sea fish among families (millions of tons).

Families	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Total	40.57	44.12	47.01	49.90	48.60	55.07	54.81	49.69	49.60	53.25
Engraulidae	8.80	10.78	11.81	12.54	11.09	14.57	12.74	6.52	4.05	6.04
Clupeidae	8.03	8.00	7.80	7.85	7.00	7.02	6.83	6.66	7.12	7.68
Herring	4.60	4.61	4.36	3.85	3.00	2.90	2.63	2.35	2.53	2.00
Gadidae	6.79	7.31	8.37	9.61	9.92	10.53	10.68	11.45	11.94	12.70
Cod	2.83	2.98	3.32	4.14	3.81	3.33	3-06	2.89	2.69	2.97
Pollock	1.04	1.22	1.74	2.20	2.55	3.06	3.59	4.21	4.62	4.91
Hake	1.11	1.29	1.72	1.43	1.30	1.52	1.53	1.88	2.13	1.79
Other	1.76	1.82	1.58	1.84	2.26	2.62	2.50	2.47	2.50	3.03
Scombridae	1.30	1.62	2.30	2.64	2.75	2.87	2.94	2.83	3.07	3.19
Thunnidae	1.10	1.21	1.28	1.30	1.32	1.22	1.34	1.48	1.61	1.67
Carangidae	1.55	1.47	1.46	1.41	1.51	1.85	2.09	2.10	2.42	2.50
Pleuronectidae	0.96	1.09	1.21	1.16	1.28	1.31	1.38	1.30	1.25	1.18
Other	12.04	12.64	12.78	13.39	13.73	15.70	17.17	17.35	17.96	18.66

has greatly increased, whereas the catch of North Atlantic, Japanese and Mexican anchovy has remained at approximately the same level (see Table 8).

Among the Clupeidae, the ocean herring, menhaden, and sardines are of greatest commercial significance.

The catch of all Clupeidae at the present time consists primarily of ocean herring (Atlantic and Pacific), with the Atlantic yielding the greatest number (Table 9). The population of both species fluctuates widely under the influence of both natural factors and fishing.

In recent years, the reserves of most schools of Atlantic and Pacific herring have been deeply depressed, their total catch dropping by 50% between 1966 and 1975, to $2.5 \cdot 10^6$ t. Such reserves of herring as the Arctic-Norwegian, Korf-Karaginskiy, Sakhalin-Hakkaido, Gizhiga, etc. once so numerous have been completely exhausted and no longer support any significant commercial fishing. There is a real danger that, unless effective measures are taken in the next few decades, it may prove impossible to restore many populations of herring, and a further reduction in their reserves will occur. Some twenty nations are involved in fishing for Atlantic herring, but the greatest catches during productive years were those of the USSR ($700\text{-}780 \cdot 10^3$), Norway ($1.2 \cdot 10^6$ t), Iceland ($770 \cdot 10^3$ t) and Denmark ($280\text{-}360 \cdot 10^3$ t). The Pacific herring is caught primarily by the USSR ($320\text{-}460 \cdot 10^3$ t), Japan (about $100 \cdot 10^3$ t) and Canada. The littoral-estuarine menhaden is found along the Atlantic coast of the USA and in the Gulf of Mexico, is fished exclusively by American fishermen and is used for the preparation of nutrient flour.

Sardines are traditionally fished by Portugal, Spain, Morocco, France, Italy and other countries; the size of the sardine catch has not significantly changed in recent years (Table 10).

Furthermore, beginning in 1971, an increase has occurred in the population of the Japanese sardine or ivasa, which, during the prewar years (1939-1940) supported an annual catch of about 2 million tons. In 1976, its catch reached $0.8 \cdot 10^6$ t, and there is every reason to believe that it will continue to increase in the future. However, in the next few years, as a result of further reduction in the catch of sardines and sardinella off the coast of Africa, the decrease in the population of Atlantic and Pacific herring, the decrease in the total world catch of Clupeidae will continue. Only the organization of fishing for Clupeidae off the coast of South America and Australia, plus an increase in the catch of the Japanese sardine, can stop this process. Since 1972, the Gadidae have occupied first place in world fishing, primarily due to the increase in the catch of pollock, tresochka esmarka, saithe and several species of hake (Table 11).

The catches of Atlantic and Pacific cod, composing one-third of the total catch of Gadidae, have been greatly reduced as a result of the depression in the stock of fish in the Atlantic. The catches of far eastern cod have increased somewhat, but are far from the potential

Table 8. World anchovy catch (millions of tons).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
North Atlantic	338	331	342	317	313	480	518.	561	749	624
Japanese	473	436	456	430	502	420	418	475	492	464
Argentine	17	11	13	32	16	14	21	41	34	30
North Pacific	3	28	32	14	62	88	41	68	104	115
Peruvian	7,681	9,621	10,530	11,282	9,711	13,060	11,237	4,815	1,960	3,965
Cape	178	160	298	331	397	404	395	417	580	598
Mexican	42	66	61	69	13	34	53	41	54	57
Other	65	64	73	65	72	66	60	98	136	190
Total	8,797	10,767	11,805	12,540	11,086	14,566	12,743	6,516	4,049	6,043

Table 9. World catch of Clupeidae (thousands of tons).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Ocean herring	4,600	4,610	4,364	3,851	2,999	2,902	2,628	2,353	2,526	2,526
Sardines	2,182	2,251	2,440	2,839	2,723	2,575	2,380	2,582	2,375	3,366
Sprats	187	216	159	174	208	241	307	334	517	655
Menhaden	791	609	549	637	716	855	1,021	920	912	923
Others	271	293	286	351	358	445	503	471	358	725
Total	8,031	7,979	7,798	7,852	7,004	7,018	6,834	6,662	7,188	7,673

Table 10. World sardine catch ($t \cdot 10^3$).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Sardinella	218	242	297	310	552	1,023	809	984	826	989
Indian	336	308	317	370	253	299	311	216	163	177
Japanese	9	14	17	24	21	17	58	58	300	351
Californian	21	19	29	27	30	36	51	54	65	81
Chilean	50	64	125	99	121	69	121	138	248	475
South African	985	940	1,043	1,492	1,227	607	393	509	473	613
European	561	662	604	515	517	480	518	561	749	624
Other	2	2	2	2	2	2	6	7	3	4
Total	2,182	2,251	2,440	2,839	2,723	2,575	2,280	2.582	2,875	3,366

Table 11. World Gadidae catch ($t \cdot 10^3$).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Cod	2,880	2,987	3,323	4,137	3,812	3,329	3,057	2,889	2.688	2,967
Pollock	1,042	1,221	1,736	2,202	2,552	3,057	3,589	4,213	4,617	4,907
Haddock	748	729	434	484	962	914	506	547	621	581
Tresochka Esmarka	77	73	198	499	170	309	400	525	500	895
Putassu	26	27	30	27	37	38	81	42	42	38
Saithe	410	454	421	356	450	641	631	655	658	716
Arctic Cod	--	1	4	2	134	268	348	167	82	125
Whiting	184	240	187	227	278	228	166	161	208	264
Tusk	44	36	39	38	28	30	32	35	47	49
Hake	1,105	1,296	1,719	1,435	1,302	1,521	1,527	1,882	2,131	1.794
Other	275	245	227	198	199	193	290	339	345	361
Total	6,791	7,309	8,368	9.609	9,924	10,528	10,677	11,455	11,939	12,697

possible reserve.

The catch of hake almost doubled in 1965-1973. However, in spite of the great intensity of fishing, the catch of most species of hake (silver hake, patagonian hake and European hake) has decreased or held steady. The supply of hake along the Pacific coast of North and South America is still in good condition, as is the reserve off the coasts of South Africa.

The catch of Pacific pollock, now widely used for the preparation of nutrient flour and stuffing, is rapidly increasing; the catch of this fish is now approaching 5 million t, 80% being accounted for by Japan. In recent years, the stock of pollock in Korea Bay and Petr Velikiy Bay, off the coast of Hokkaido, Sakhalin, Kamchatka and in the eastern portion of the Bering Sea, has been intensively used. We must assume that no less than 10 million tons of pollock are consumed by the Pacific Ocean seals each year. Reports are already being heard of significant decreases in the average age of many populations of pollock; therefore, a further increase in catch can occur only if the populations of the northwestern portion of the Bering Sea and the Gulf of Alaska, still incompletely utilized, can be brought into play.

The catch of other Gadidae can be significantly increased by development of fishing for hake within the regions mentioned above, as well as the eastern Pacific, off South Africa and the Patagonian Shelf, by fishing for poutassou in the North and South Atlantic, and Arctic cod in the Barents Sea. At the same time, the catch of cod, haddock, silver and red hake in the traditional fishing regions of the North Atlantic will decrease, while the total catch of pollock and hake in the Pacific Ocean will remain at approximately its present level. The number of commercial species of Gadidae as yet plays a secondary role in commercial fishing: whiting--catch up to $270 \cdot 10^3$ t, tresochka esmarka--up to $900 \cdot 10^3$ t, tusk--$30\text{-}50 \cdot 10^3$ t, poutassou--$40\text{-}80 \cdot 10^3$ t, etc., although in most cases the size of the catch does not correspond to the population of these fish at all. This is a result of the low economic effectiveness of fishing for these species, due to the relatively low quality of their meat.

The development of sea fishing with the extensive use of trawls at different depths, purse seines, longlines and other hook equipment has led to a rapid increase in the catch of a number of pelagic fish, including many species of the Carangidae and Scombridae. At the present time, both of these groups support a total catch of about 5 million tons, significantly greater than the catch of Thunnidae, Salamonidae, Pleuronectidae, etc. The catch of Scombridae has increased from $1.3 \cdot 10^6$ t in 1965 to $3.2 \cdot 10^6$ t in 1975. Representatives of this group inhabit primarily the neritic zones. Of the world catch of Scombridae, 56% consists of the Japanese mackerel, 34% of the common mackerel and 10% of the Indian mackerel (data for 1973). A significant fraction of the catch of mackerel is taken by Japan--up to $1.4 \cdot 10^6$ t, while a large quantity, as much as $480 \cdot 10^3$ t is caught by Norway, significantly less by the USSR, France and South Africa. The extremely rapid growth of the Norwegian catch of mackerel (from 23,000 t in 1963 to 480,000 t in 1966) is explained by the high population of this fish off the coast of Norway and the use of purse seines, which accounted for 455,000 t. The Soviet Union has greatly intensified its fishing for mackerel in recent years, in the northwestern Pacific (to 80,000 t) and off West Africa (to 150,000 t). Doubtless, mackerel fishing is quite promising.

The catch of Carangidae had increased by a factor of 16 by 1970 in comparison to the prewar level (1938), and there is every reason to assume the possibility of further increases. Thus, off the coast of Japan in some years the catch of this fish has even been artificially held down. Large accumulations of mackerel have recently been found off the Tasmanian coast. In the opinion of many scientists, it will be possible to catch as many as 1 million tons of pelagic fish per year near New Zealand, including many Carangidae. The greatest quantity of Japanese mackerel are caught in the East China Sea and off the coast of Japan ($510-560 \cdot 10^3$ t), as well as in the Philippines ($100 \cdot 10^3$ t). Other species of Carangidae are caught off the west coast of Africa, where fishing is conducted primarily by ships of the USSR ($180 \cdot 10^3$ t), Angola ($170 \cdot 10^3$ t) and Spain ($70 \cdot 10^3$ t).

A lesser role in the sea fish catch (up to $1.7 \cdot 10^6$ t) is played by the tuna, although due to the high value of the meat of this fish, tuna fishing is significantly more successful economically than fishing for most other types of fish. Therefore, the tuna catch develops from year to year, and at the present time is conducted in the open Pacific, Atlantic and Indian Oceans. Tuna inhabit the great water areas of the ocean, forming no dense accumulations, making it more difficult to catch them. However, information on the results of tuna fishing indicates that the trend is doubtless toward decreasing effectiveness (Table 12). For example, the catch of yellowfin and blue-finned tuna decreased from 8 fish per 100 hooks on a longline in 1950 to 2 in 1965. The reserves of large tuna are being caught with great intensity in almost all regions of the ocean, and the only hope for any significant development of tuna fishing lies in more intensive fishing of the smaller and stripe-bellied tuna.

The overwhelming majority of tuna (50-60%) is caught by Japan. Significantly smaller quantities are caught by the fisherman of the USA, France, Spain and Peru. The Soviet Union catches but a few thousands of tons of the valuable fish.

When tuna is fished using longlines, swordfish and sharks are caught in large quantities. Sharks, rays and chimaera are also the objects of a specialized fishing industry. The annual catch of sharks in recent years (1968-1975) has held steady at a level of about $400 \cdot 10^3$ t, of rays at $90-140 \cdot 10^3$ t. This is much less than their actual reserves. The shark catch in the World Ocean could be at least doubled.

In addition to the commercial fish mentioned above, the world catch includes many representatives of various families of demersal fish, caught during trawling and other types of bottom fishing: Pleuronectidae (see Table 8), sea perch, *Ammodytes*, etc. (Table 13).

Table 12. World catch of tuna ($t \cdot 10^3$).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Albacore	199	194	247	187	189	159	212	237	240	226
Blue-finned tuna	117	116	120	120	129	116	132	142	141	142
Common tuna	109	102	105	99	103	85	95	88	98	98
Mackerel tuna	44	42	42	33	38	56	66	64	57	49
Stripe-bellied tuna	267	350	376	326	320	371	408	404	519	588
Spotted tuna	32	45	30	41	39	14	9	9	7	13
Yellowfin tuna	256	275	244	330	335	327	307	395	377	373
Other	79	89	119	162	163	96	106	139	175	178
Total	1,103	1,213	1,283	1,298	1,316	1,224	1,335	1,478	1,614	1,667

Table 13. World catch of various benthic species ($t \cdot 10^3$).

Species	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974
Sciaenidac	350	283	271	315	256	412	394	427	476	550
Sparidae	306	288	353	320	251	329	326	370	374	342
Ammodytes	254	254	317	356	228	419	667	560	501	831
Scorpaenidae	945	782	694	576	563	541	620	604	615	550
Mackerels	115	111	86	112	133	1,949	1,715	1,783	1,945	2,093
Total	3,217	3,264	3,290	3,330	3,170	3,894	3,906	3,965	4,061	4,687

The overwhelming majority of these fish, inhabiting the shelf or the upper portion of the slope, have long life cycles and relatively low reproductive capacity which, in combination with intensive fishing, has led to a decrease in the population of many species of fish, particularly the plaice and sea perch. Doubtless, a significant increase in the catch of certain benthic fish, such as sand eels, is possible. However, the fact that the overwhelming majority of these species are littoral, shallow-water fish which form significant numbers of small, local populations, makes this group of fish suitable primarily for coastal fishing.

There are other fish which are promising for the development of fishing. They include primarily representatives of the Sauridae--the sauries, widespread in the North and South Atlantic and in the Pacific (saury fishing is being successfully conducted by Japan and the USSR, bringing in as much as $300\text{-}500 \cdot 10^3$ t in some years). No less promising is fishing for capelin, the catch of which in the Sea of Norway and the Barents Sea and in the region of Newfoundland has exceeded 200 million tons in recent years. Representatives of the family Myctophidae are also quite numerous, with large accumulations of these fish found by the bottom and depths of 500-900 m in various regions of the ocean, particularly off the Pacific coast of Japan.

The invertebrates are of much less significance in the world seafood picture, representing about 8% ($5.8 \cdot 10^6$ t) of the total world seafood catch. Of this quantity, 65-70% consists of mollusks, about 30% ($1.9 \cdot 10^6$ t) crustaceans, and about $70 \cdot 10^3$ t of Echinodermata and others. The world catch of invertebrates is growing slowly (Table 14).

Mollusks are caught in the largest quantity off the coast of Japan--up to $1.4\text{-}1.6 \cdot 10^6$ t, primarily squid and bivalves. A large quantity ($0.6\text{-}0.7 \cdot 10^6$ t) of mollusks is caught in the USA, mostly oysters ($0.3\text{-}0.4 \cdot 10^6$ t), abalone ($0.2 \cdot 10^6$ t) and scallops ($0.1 \cdot 10^6$ t). The USA takes approximately half of the entire world catch of oysters, Japan and France representing a large fraction of the remaining catch. Mussels are caught primarily by European fishermen (about 85% of the total catch), predominantly from the Netherlands (up to $120 \cdot 10^3$ t), Spain ($70 \cdot 10^3$ t) and France ($30\text{-}40 \cdot 10^3$ t). One of the most valuable mollusks is the scallop, which is primarily caught in the northwestern Atlantic off the coast of the USA by fishermen from Canada ($60\text{-}70 \cdot 10^3$ t) and the USA ($70\text{-}80 \cdot 10^3$ t). A significantly smaller quantity of scallops (about 7,000 t) is caught by Japan and by Australia. The prospects are obviously favorable for the development of the mollusk fishing industry, particularly squid, as well as small bivalve mollusks (used as feed in animal husbandry) in many regions of the ocean.

Among the crustaceans, first place is occupied by shrimp. The largest catches are brought in from the Gulf of Mexico, the Caribbean, the coasts of Japan and India, and the Bering Sea. Following shrimp, in terms of catch, are the crabs (primarily the Kamchatka crab), then the lobsters. The intensity of fishing for the Kamchatka crab and the lobster threatens depletion of the reserves and requires that additional measures be taken to regulate fishing. The resources of shrimp and

Table 14. World catch of invertebrates ($t \cdot 10^3$).

Types	1938	1948	1958	1961	1965	1970	1973	1974
Mollusks	1,200	1,340	2,070	2,500	2,951	3,223	3,399	3,391
Crustaceans	600	620	859	990	1,205	1,585	1,799	1,887
Echinodermata	17	8	34	34	48	72	65	61
Total	1,817	1,968	2,954	3,524	4,204	4,880	5,263	5,339

Atlantic lobsters will allow the catch to be increased in a number of regions.

The annual catch of Echinodermata is about 70,000 t, of which some 60% consists of sea urchins.

Marine vegetation--algae and marine grasses--are taken in large volumes from the shallow waters of the World Ocean (about $1.2 \cdot 10^6$ t), about 70% being grown and taken in Japan.

As concerns the whales, due to the great decrease in the population of the largest toothed whales--the blue whale, fin whale and humpback whale--in recent years fishing for smaller whales has been developed, primarily the sei whale and minke. The total weight of whales caught decreases from year to year.

This, in general terms, is the current volume and composition of the catch of seafood in the World Ocean.

The current level of intensity of utilization of the reserves of most traditional hunted objects in the World Ocean, in many cases, is quite high, but in many regions it can be significantly increased.

Analysis of the information we have presented shows that the intensity of commercial utilization of most of the main commercial species of fish, particularly the cod, sea perch, plaice and herring, which are the most sought-after fish in the northern hemisphere, has in most regions reached or almost reached its limit, and any increase in the catch will occur only as a result of an increase caused by such natural factors as may increase the population of individual generations making up the total world population. This is particularly true of the northwestern and northeastern sections of the Atlantic, and the northern and north-central sections of the Pacific. Naturally, the catch of such demersal fish as the macrourus pollock, Arctic cod, Pacific cod and certain other benthic fish may be increased even here. However, this increase will be relatively slight and can only compensate for the decrease in results of fishing in the most important regions to a small extent.

The greatest increase in the catch of benthic fish can be expected primarily within the tremendous area of the Falkland-Patagonian shallows, where the catch of hake, poutassou, macrourus and certain others may become as great as 3 million tons. The New Zealand plateau, the eastern and southern coasts of Australia and the Pacific coast of South America represent smaller, though still significant possibilities for increasing the catch of benthic fish. All remaining regions in the World Ocean can provide only a slight increase in the catch of benthic and deep-water fish in comparison to the levels already achieved. The total possible increase in the catch of benthic and deep-water inhabitants within the relatively shallow areas of the World Ocean may be about $4\text{-}5 \cdot 10^6$ t, of which most will come from the regions which we have already mentioned. A significantly greater increase in the catch--up to $17\text{-}20 \cdot 10^6$ t--can be expected from the catching of fish and other animals which lead a pelagic mode of life and primarily inhabit the highly productive neritic areas and the adjacent portions of the oceanic zone. These are primarily sardines and other similar species, anchovies, Carangidae, Sauridae, small tunas, Myctophidae, squids and certain others. Judging from the level of use of these animals achieved to date in some of the neritic regions of the ocean and data on their distribution and population in other regions, we can assume the possibility of a significant increase in their catch in all oceans, particularly off the coast of Australia, in the northern, west-central and east-central parts of the Pacific and southwest Atlantic oceans. The prospects for the central oceanic regions are more limited.

Judging from the status of the biologic resources of the World Ocean, we can present the following, quite approximate figures for the probable increase in the world catch of the most important groups of ocean fish (Table 15).

Table 15. Probable increase in world seafood catch ($t \cdot 10^6$).

Group	1974 Catch	Probable Increase in Catch	Probable Catch
Pelagic species	38.3	21.0	59.3
Engraulidae	6.0	7.0	13.0
Clupeidae	7.7	1.7	3.0
Carangidae	2.5	2.1	4.6
Scombridae	3.2	0.3	3.5
Sauridae	0.5	2.0	2.5
Thunnidae	1.7	1.1	2.8
Euselachiae	0.6	0.4	1.0
Teuthoidea	1.1	2.9	4.0
Other	15.0	1.5	18.9
Benthic objects	21.7	5.7	27.4
Gadidae	12.7	2.3	15.0
Pleuronectidae	1.2	0.0	1.2
Macruridea	0.6	0.9	1.5
Other (including invertebrates)	7.2	2.5	9.7
Total	60.0	26.7	86.7

In most regions, the probable increase in catch will occur primarily due to an increase in the catch of inhabitants of the upper portion of the slope and elevations of the ocean floor--macruri, macruroni, hake, lemonema, etc., in warm-water regions of the shelf--due to an increase in the catch of the numerous species of Carangidae, Sciaenidae, etc. To a significantly lesser extent, we can expect an increase in the catch of poutassou, saithe, haddock, pollock, cod and hake. A significant increase in the total volume of the catch may be accounted for by inhabitants of the waters of Australia and New

Zealand--Beryciformes, etc. In the neritic zone, most promising for the development of fishing are the Engraulidae, Carangidae, Scombridae, sardines, and, in adjacent regions of the oceanic zone--small tuna, sauries, Myctophidae, Teuthidea and certain other species. Finally, in the oceanic zone itself (in the epipelagic zone), the most important objects for a developing fishery may be the large and small tuna, marlins, swordfish, dorados, sauries, sharks, flying fish and squids. Thus, the prospects for the development of world fishing can be rather clearly seen--primarily due to an increase in the catch of pelagic seafood.

In spite of the exceptionally great quantity of certain species of anchovy currently taken from the ocean, we can expect an intensification of anchovy fishing off the coasts of Argentina and Mexico, which may yield approximately 3 million tons. We should keep in mind that the population of anchovies and sardines is subject to great fluctuations and, therefore, the possibility must be considered of great, at times catastrophic, decreases in the catch, as has occurred with the Peruvian anchovy, Japanese and California sardines. There are doubtless possibilities for increasing the sardine catch and the catch of similar forms near the coast of Africa and Australia, and also of certain species of Carangidae and Scombridae in various regions of the ocean. There is every reason to believe that in the epipelagic zone of the northern and southern areas of the Pacific and Atlantic Oceans, there are large numbers of Sauridae, of which the northern Pacific saury, perhaps, is the most numerous. If we can find effective methods for creating artificial concentrations of this fish in open regions of the ocean, where it is quite scarce, the saury catch may be significantly increased.

A significant increase in the catch may also occur by the development of the catch of small tuna, the reserve of which is as yet underutilized in many regions of the ocean. There is no reason to expect a great increase in the catch of large types of tuna. The shark catch can be doubled, but the total volume of this catch will not be high in the near future.

Among the pelagic fish promising for fishing purposes we must include the capelin, flying fish, Australian salmon, dorados, Myctophidae, etc. Fishing for squid seems quite promising, since the reserves of this animal would allow its total catch to be increased by many times.

More intensive fishing for pelagic animals would allow an increase in the catch by 20-25 million tons.

1.3 Regional Placement of Marine Fish

The geography of the world fishing industry, i.e., the use of the raw materials base in various regions, like the fluctuations of the numbers of commercially fished objects and the status of their reserves, can influence the composition of the catch and the results of fishing. Contemporary fishing-economy statistics are based on the division of the World Ocean into statistical regions by the FAO.

As we present the fishing-economy characteristics of the most significant regions of the World Ocean, we shall use these generally accepted divisions (Table 16).

Fishing is conducted with the highest yields in 4 regions of the World Ocean: the North Atlantic, North, West-central and Southeastern Pacific, the total area of which represents some 26% of the total water area of the oceans, but yields some 80% of the total world catch.

The Atlantic Ocean is the most productive of the 3 oceans. In 1970, the catch taken from the Atlantic Ocean totalled 26 million tons, for a fish productivity of 260 kg/km^2, significantly higher than the productivity of the Pacific Ocean (170 kg/km^2) or Indian Ocean (40 kg/km^2).

The Northeastern Atlantic, including the North Sea, Baltic Sea, Sea of Norway, Barents Sea and White Sea is a traditional, exceptionally productive fishing region in the World Ocean. About 60% of the water area here covers depths of less than 1,000 m. The total catch here exceeded 11 million tons, doubling since the war, and now represents 20% of the world catch. This region is particularly important for the fishing industry of the USSR (Table 17).

The catch in this region increased until 1966. In subsequent years, as a result of the great decrease in the reserves of herring and cod, the total catch of all countries has stabilized. The intensity of fishing for most species has reached the saturation point and only the poutassou, Scombridae, Arctic cod, capelin and certain other fish can increase. The total catch of the Soviet fishing industry in this region in 1974 reached 2 million tons.

North Sea--one of the most productive regions of the World Ocean. The high biomass of the benthos and zooplankton, consisting primarily of edible species, and the predominance in the composition of the ichthyofauna of rapidly growing planktonophages and benthophages, with the limited population of predators, assure high fish productivity which, in combination with other favorable conditions, allows the fishermen of many countries to achieve high and comparatively stable catches and to increase the yield of fish products per unit area to a very high level (5.5 t/km^2), approaching the first productivity of the Azov Sea prior to the regulation of the runoff of the Don and Kuban' Rivers (8.2 t/km^2). Of all commercially fished seafood, the pelagic planktonophagous fish, primarily herring, sprat, and mackerel, occupy the leading position. Among the benthic, primarily benthophagous fish, the plaice and Gadidae (cod, haddock, whiting, saithe, tresochka esmarka) and others are most numerous. Most fish caught in the North Sea are permanent inhabitants of the Sea, but a certain small quantity enters the Sea through La Manche (mackerel) and from the Sea of Norway (herring of the Norway stock).

Fishermen of many nations fish the North Sea, including those of the USSR. The Soviet catch in some years approaches 500,000 t (1973--230,000 t). It consists primarily of herring, sprat and haddock. The

Table 16. Geographic distribution of the catch of seafood in the World Ocean (1973).

Region	Catch of all Countries		Catch of USSR		
	$t \cdot 10^6$	%	$t \cdot 10^6$	% of Catch of all Countries	% of USSR
Atlantic Ocean	25.6	45.7	4.86	19.0	62.6
Northwest	4.5	8.0	1.36	30.2	17.5
Northeast	11.2	20.1	1.61	14.4	20.7
West-central	1.4	2.5	0.009	0.7	0.1
East-central	3.5	6.2	0.94	26.9	12.1
Mediterranean and Black Sea	1.1	1.9	0.29	26.4	3.7
Southwest	0:8	1.4	1.01	+	+
Southeast	3.1	5.6	0.65	21.0	8.4
Indian Ocean	2.7	4.8	0.05	1.9	0.6
West	1.8	3.2	0.04	2.2	0.6
East	0.9	1.6	0.01	+	+
Pacific Ocean	27.6	49.5	2.86	10.4	36.8
Northwest	16.3	29.2	2.23	13.7	28.7
Northeast	1.9	3.4	0.38	20.0	4.8
West-central	5.1	9.1	—	—	—
East-central	1.1	2.0	0.14	12.7	1.8
Southwest	0.3	0.6	0.07	23.3	0.9
Southeast	2.9	5.2	0.04	1.4	0.5

Table 17. Catch of seafood in Northeast Atlantic ($t \cdot 10^3$).

Region	1965	1966	1967	1968	1969	1970	1971	1972	1973
All Countries	9,370	10,045	9,984	10,056	9,780	10,580	10,362	10,648	11,143
USSR: Total	1,048	1,148	1,119	1,146	1,470	1,566	1,377	1,272	1,611
% of all Countries	11.2	11.4	11.2	14.1	15.0	14.9	13.3	11.9	14.5
Barents Sea	192	253	351	615	594	532	501	474	669
Sea of Norway	548	467	286	137	15	69	75	4	3
North Sea	63	156	107	125	326	483	203	157	230
Baltic Sea	184	208	220	253	279	298	314	338	329
Other regions	61	64	155	286	256	193	284	299	380

degree of commercial utilization of the fishing resources of the North Sea, particularly herring, is approaching the ultimate limit.

Baltic Sea. The fish productivity of the Baltic Sea is relatively low, slightly over 1 t/km^2. Some $0.7 \cdot 10^6$ t of fish are removed from the sea each year, including $0.3 \cdot 10^6$ t by the USSR. The commercial ichthyofauna of the Baltic Sea consists primarily of massive planktonophages--the Baltic herring and sprat, Baltic cod, feeding on macroplankton and benthos, plus typical benthophages--the plaice. Furthermore, we also find salmon, whitefish, vimba, eel, etc. The fish resources of this sea are rather intensively utilized. The fish productivity of its individual regions differs greatly: in Botnicheskiy Bay, it is 0.5-0.6 t/km^2, in Kurshskiy Bay, about 9 t/km^2. In 1973, the countries surrounding the Baltic Sea signed a convention calling for joint development and application of measures for the regulation of fishing in order to assure efficient utilization of the biologic resources of the sea.

Barents Sea. The abundance of food in the form of benthos and plankton, in combination with the favorable oceanographic characteristics, makes the Barents Sea a region of permanent residence or seasonal feeding of Arctic fauna (Arctic cod, saffron, cod, polar plaice), Subarctic fauna (capelin) and Boreal fauna (cod, haddock, saithe, herring, sea perch, common plaice, etc.). More warm-water fish also find their way here: mackerel, whiting, etc. Representatives of the Arctic fauna inhabit primarily the cold-water eastern regions of the sea, while the Boreal species remain in the more warm-water western sections.

The cod, haddock, Arctic cod, sea perch, herring and capelin are of predominant significance for fishing, making up as much as 95% of the total catch. The catch of the USSR in 1968-1969 reached $0.6 \cdot 10^6$ t, then greatly decreased in subsequent years as a result of a significant decrease in the population of herring from the Arctic and Sea of Norway, cod, haddock and sea perch. At the same time a significant increase has been observed in the population of Arctic cod and capelin, the total catch of which by fishermen of all nations reached 2 million tons in 1970-1975.

The northeast portion of the Atlantic Ocean also includes the Sea of Norway and the Greenland Sea, the waters of Iceland, Ireland and the Bay of Biscay, that portion of the Atlantic adjacent to the Iberian Peninsula, as well as the open regions of the ocean. Here we find herring, cod, haddock, sea perch, mackerel, poutassou, sardines, squids, etc. Very intensive fishing of herring from the Arctic and Sea of Norway, particularly the huge catch of small, immature fish by Norwegian fishermen, the so called "fat" herring, has led to exhaustion of the reserve of this once most numerous stock of ocean herring and practically complete cessation of fishing within the limits of the Sea of Norway. Only in recent years has some increase in the population of herring in these waters been observed.

The level of utilization of the raw materials available to the fishing industry in this region is rather high, and, for many species (herring, cod, sea perch, plaice, etc.), the maximum possible level has already been reached, or perhaps even exceeded. Steps are being taken to regulate fishing through various international conventions and agreements on fishing. However, this highly productive region of the World Ocean may slightly increase the volume of its production by the development of fishing of certain underutilized species: poutassou, capelin, saithe, mackerel, squids, etc.).

Northwest Atlantic. An exceptionally important fishing region with a total area of 4 million km^2, of which 27% is made up of water less than 1,000 m in depth.

For many centuries, accumulations of cod have been fished off the banks of Newfoundland, and beginning in the mid 1950's, very intensive fishing off Georges Bank was begun, taking herring, sea perch, haddock, silver and red hake, plaice, halibut, macruri, capelin, squids, etc. (Table 18).

In recent years, the results of fishing here, in spite of a significant increase in fishing efforts, have not only not increased, but, in terms of certain species (sea perch, silver hake, etc.) have even decreased. The current catch ($4.0\text{-}4.7 \cdot 10^6$ t) has almost reached the maximum possible level.

Soviet fishing occupies a significant place in the total catch, utilizing primarily the resources of cod, silver hake, sea perch, herring, macruri, capelin, etc. By 1974, the Soviet catch reached $1.16 \cdot 10^6$ t (over 30% of the total catch). Soviet fishing studies have revealed accumulations of sauries in the southern portion of this tremendous region, the population of which is high, and fishing for which seems quite promising.

Also promising is fishing for squid, which form great concentrations along the shores of Newfoundland, on the shelf off Nova Scotia, Georges Bank and in the region of New York.

Intensification of the catch of sauries, capelin, squid and other little-used fish and invetebrates will allow some increase in the total volume of the catch. The development of recommendations for efficient and effective utilization of the fishing resources is the job of the International Commission on Fishing in the Northwest Atlantic.

The Central Atlantic. Among the commercial seafood in this area, the inhabitants of the pelagic zone predominate--sardines, horse mackerel, mackerel, tuna, etc. Among the fish leading a benthic mode of life, the Cyprinidae (carp) and Sciaenidae predominate. About 5 million tons of seafood is caught in this area, primarily sardines, mackerel and sea carp.

In 1974, the Soviet catch was $1.17 \cdot 10^6$ t, about 12% of the total catch of the USSR and 15% of the total catch of all countries in this

Table 18. The catch of seafood in the Northwestern, Central, and South Atlantic ($t \cdot 10^3$).

Region	1965	1966	1967	1968	1969	1970	1971	·1972	1973	1974
Northwest										
Total	4,021	4,020	4,073	4,674	4,486	4,240	4,370	4,330	4,490	4,020
USSR	853	842	624	801	986	812	1,022	1,150	1,357	1,157
%	21.2	20.9	15.2	17.1	21.9	19.1	23.4	26.3	30.2	23.8
West-central										
Total	1,381	1,256	1,287	1,365	1,413	1,410	1,620	1,480	1,360	1,500
USSR	51	37	24	7	5	--	11	74	9	26
%	3.6	2.9	1.8	0.5	0.3	—	0.6	5.0	0.6	1.7
East-central										
Total	1,221	1,368	1,545	1,684	2,094	2,980	3,030	3,260	3,430	3,660
USSR	82	79	154	319	570	613	790	849	943	1,145
%	6.7	5.7	10.0	13.9	27.2	21.6	26.8	26.9	27.1	31.3
Southwest										
Total	524	644	1,261	815	701	1,080	760	860	860	860
USSR	--	73	673	190	93	421	26	5	6	13
%	—	11.3	53.7	23.3	13.2	38.9	3.4	0.6	0.7	1.5
Southeast										
Total	2,217	2,380	2,637	3,289	3,055	2,470	2,430	2,960	3,080	2,930
USSR	361	361	251	485	407	423	439	720	649	448
%	16.3	15.2	9.5	14.7	13.3	17.1	18.0	24.3	21.1	15.8
Total Catch in all Regions	19,937	20,886	22,199	23,063	22,613	23,990	23,750	24,730	25,670	26,140
USSR	2,647	2,847	3,150	3,503	3,669	4.137	3,929	4,354	4,861	5,156
%	13.2	13.6	14.1	15.1	16.2	17.3	16.6	17.7	19.0	19.7

region. The low level of fish productivity of this tremendous ocean region means that the take of fish products at the present time averages about 180 kg/km^2, an order of magnitude less than in the northeast portion of the ocean. In the most productive areas--the Caribbean, Gulf of Mexico, near the Antilles, off the northwest coast of Africa and in the Gulf of Guinea--the catch rises to 400-500 kg/km^2. Studies have shown that the current catch in the tropical zone of the Atlantic Ocean could be almost doubled.

The South Atlantic has an area of 47 million km^2, of which 10.2% is represented by depths of less than 1,000 m. The shallowest plateau (about $1.4 \cdot 10^6$ km^2) is the Patagonian-Falkland shelf, adjacent to the Atlantic coast of Uruguay and Argentina. The great extent of this region in latitude allows both warm-water (tuna, marlin, swordfish, sardines, etc.) and cold-water (poutassou, hake, nototheniids) fish to live here. The intensity of fishing is high only along the southwest and south coasts of Africa, where sardines are caught in large quantities ($0.7 \cdot 10^6$ t), as well as anchovies ($0.4 \cdot 10^6$ t) and hake ($0.8 \cdot 10^6$ t), whereas on the Patagonian shelf, the fish resources of which would allow up to 5-6 million tons of fish to be taken each year, fishing is little developed (only about $0.6 \cdot 10^6$ t are removed each year). The total catch of the South Atlantic is about 4 million tons, the total possible catch--over 9 million tons. In recent years, the Soviet trawler fleet off the southwest coast of Africa has caught 400-$720 \cdot 10^3$ t of fish, primarily hake and horse mackerel.

The regions near the Antarctic, inhabited by commercial quantities of whales, seals, certain fish and particularly small planktonic crustaceans--krill--are of great significance for fishing. Of the fish which have or could have commercial significance in the Antarctic waters, we need note only the species of the nototheniids, and white-blooded fish. Furthermore, during the warm season, poutassou reaches this area from the southern portion of the Patagonian shelf, attracted by the large concentrations of krill, used as food by almost all the inhabitants of the Antarctic, particularly the whales. The reserves of krill here are tremendous, amounting to many hundreds of millions of tons. Whales alone, during the period of their high population, consumed over 100 million tons of krill each year.

Summarizing the estimate of the raw-material basis for the fishing industry in the Atlantic Ocean, we should note that the catch of all countries in this basin can be increased to 36-37 million tons, 10 million tons greater than the current level (as of 1973). The Soviet Union catches about 5 million tons in the Atlantic, i.e., 63% of the total catch of ocean fish.

The Pacific Ocean provides up to one half of the world catch of seafood (27-35 million tons, Table 19). The catch here is dominated by pelagic objects (89%, as opposed to 55% in the Atlantic Ocean). The current level of fishing productivity of the Pacific Ocean (170 kg/km^2) is lower than that of the Atlantic Ocean (260 kg/km^2) and the possibilities for further increasing the catch are considerable.

Table 19. Catch of seafood in the Pacific Ocean ($t \cdot 10^3$).

Region	1965	1966	1967	1968	1969	1970	1971	1972	1973	1973
Total	23,803	26,443	28,399	30,618	29,520	34,630	34,190	28,830	27,970	30,840
Northwest	10,687	10,789	11,162	12,151	12,074	12;980	14,250	14,500	16,490	16,710
USSR	1,115	1,092	1,204	1,302	1,394	1,448	1,562	1,434	2,233	2,362
Northeast	1.456	1,664	1,899	1,920	2,202	2.650	2,310	2,730	1,880	2,310
West-central	2,652	3,020	3,219	3,679	3,948	4,170	4,500	4,740	5.030	5,090
East-central	616	650	778	813	793	920	390	970	1,160	1,010
USSR	—	—	—	53	25	20	2	13	138	22
Southwest	119	154	159	167	218	170	220	270	320	410
USSR	—	—	—	—	—	—	10	54	74	89
Southeast	8,273	10,166	11,182	11,888	10,285	13,740	12,020	5,570	3,090	5,310
USSR	—	—	—	—	—	—	—	35	39	—

In the northern portion of the ocean, to the north of 40°N and in the adjacent seas, $19.2 \cdot 10^6$ t of seafood is caught (1975 figures) i.e., two thirds of all the catch of the Pacific Ocean. Soviet fishermen catch the predominant portion of their total Pacific Ocean basin catch here (98% in 1974), their catch representing about 3 million tons, or 15% of the total catch in the region. This catch is represented primarily by Pacific herring, sardines, anchovies, sea perch, cod, saffron cod, pollock, saury, Pacific salmon, many species of plaice and halibut, mackerel, horse mackerel, macruri, etc.

Research and prospecting work has allowed commercial exploitation of previously untouched resources in the Sea of Japan, the Sea of Okhotsk and the eastern portion of the Bering Sea, near the Aleutian Islands, in the Gulf of Alaska, along the Pacific coast of Canada and the USA, in the region of the northwest ridge, along the coast of Japan and in the open regions of the ocean. This has allowed a significant lengthening of the list of commercial fish, which now includes many dozens of species.

The Sea of Japan. The commercial ichthyofauna of the northwest portion of this sea consists of cold-water forms: saffron cod, pollock, cod, herring, plaice, mackerel, etc. Warm-water species predominate in the south: mackerel, saury, anchovies, etc. Up to 1940-1941, Pacific sardines entered the Sea of Japan in large numbers and their catch by Soviet, Korean and Japanese fishermen reached 2 million tons. In recent years, as a result of a change in oceanographic conditions in southern Japan, where the fish spawn, the number of Pacific sardines has greatly decreased. In the past few years, an increase has been observed once again in the stock of Pacific sardines, and in 1975 its catch off the coast of Japan reached 800,000 tons. Before 1943, the catch of another massive fish in the Sea of Japan--the herring of the Sakhalin-Hokkaido stock--was as great at 500,000 tons; now it has decreased to a few tens of thousands of tons, which has, to some extent, been the result of natural factors, but to a considerably greater extent, a result of the excessive overfishing of the spawning herring.

The total catch of all seafood in the Sea of Japan exceeds 1 million tons, mostly pelagic species such as mackerel, horse mackerel, anchovy, etc. (over $0.6 \cdot 10^6$ t), to a significantly lesser extent (about $0.4 \cdot 10^6$ t)--benthic species. The fish productivity of the sea is rather high: 830 kg/km^2 of benthic fish and about 70 kg/km^2 of pelagic fish. Further intensification of fishing can be achieved by some increase in the volume of the catch of Pacific sardines, horse mackerel, sauries and other fish in the southeastern portion of the sea.

Considering the warmth of the sea, there are great possibilities for the development of commercial growth of aquatic plants (sea cabbage, red laver, etc.), as well as the breeding and raising of invertebrates (scallops, mussels, oysters, trepangs) and fish.

The Sea of Okhotsk, with the exception of the most southern portion, is a cold-water sea, its ichthyofauna consisting of forms which live at relatively low temperatures. The most plentiful commercial objects are pollock, herring, cod, saffron cod, plaice, the Ammodytes, sea perch, Pacific salmon (chum salmon, humpback salmon, blue-back salmon, silver salmon, king salmon), Kamchatka crabs, beetle crabs, etc. Herring and pollock are particularly numerous here. The total catch reaches $1.6\text{-}1.8 \cdot 10^6$ t. Soviet fishermen, in recent years, have achieved catches in the Sea of Okhotsk up to 1 million t, primarily of pollock (450,000 t), herring (300,000 t), salmon (50,000 t), plaice and crabs. Seals which cluster along the southeast coast of Sakhalin and Tyuleniy Islands are hunted. In recent years, there has been a significant decrease in the population of Okhotsk Sea herring (Okhotsk-Ayansk, Gizhiginsk, Eastern Sakhalin), due to natural factors, greatly intensified by the effects of heavy fishing. Since the 1960's, a significant reduction in the reserve of Pacific salmon has occurred, primarily due to large-scale fishing by Japan.

The current fish productivity of the Sea of Okhotsk is as great as 1,300-1,400 kg/km^2. Further significant intensification of fishing is impossible, and the results of fishing can be high only in years when the population of herring, pollock and salmon is large, and also as a result of more complete utilization of the raw-material resources of cod, Ammodytes, saffron cod, capelin, mackerel, etc.

The Bering Sea. The commercial ichthyofauna consists of cod, pollock, Arctic cod, herring (Korf-Karaginskiy and Eastern Bering Sea stocks), plaice, halibut, sea perch, mackerel, Pacific salmon, capelin, macruri, and coalfish. Kamchatka crabs are found in large numbers, as well as beetle crabs (particularly in the eastern portion of the sea and in Olyutorskiy Bay) and shrimp. Seals nest along the Pribyl and Komandorskiy Islands, as well as on ice floes. Within the Bering Sea, fishing is conducted by the USSR, Japan, and the USA each year taking over 3 million tons, primarily of pollock ($2.2 \cdot 10^6$ t), salmon ($50 \cdot 10^3$ t), herring ($130 \cdot 10^3$ t), plaice ($120 \cdot 10^3$ t), sea perch ($100 \cdot 10^3$ t), crabs and shrimp. The Soviet Union accounts for $500\text{-}700 \cdot 10^3$ t.

The biological resources of the Bering Sea are quite intensively utilized by fishermen, and most species (plaice, sea perch, salmon, Kamchatka crabs) are under stress. The volume of fish production on the shelf is over 1,500 kg/km^2, in the pelagic zone--500 kg/km^2, i.e., it reaches the levels found in the most productive regions of the World Ocean. A further slight increase in the catch is possible by utilization of the resources of Arctic cod, capelin, mackerel, cod and pollock.

In the relatively warm-water regions of the Northeast Pacific Ocean, from the Gulf of Alaska to California, we find sea perch, pollock, cod, herring, sauries, plaice, halibut, Pacific hake and salmon. Fishing here is primarily concerned with salmon, herring, sea perch, plaice, halibut, hake, crabs and shrimp. The total catch reaches $600\text{-}700 \cdot 10^3$ t, Soviet fishermen, primarily fishing for hake, sea perch, coalfish, plaice, etc., bringing in about $250 \cdot 10^3$ t. Further development of fishing must be achieved here by intensification of fishing for hake and squid, organization of fishing for sauries, etc., with simultaneous limitations of the scale of fishing for sea perch, herring, plaice and halibut, the resources of which are already being quite intensively exploited. The significant possibility for development of saury fishing in the open regions of the ocean from the north coast of Japan to the Pacific coast of the USA is indicated by the information from fishing research studies and prospecting work undertaken in recent years.

The total volume of the catch in the North Pacific Ocean can be significantly increased by fishing for pelagic species (saury, capelin, sand eels, squids, etc.), the reserves of which are still underutilized.

The central portion of the Pacific, from 40°N to 10°S, includes water from Japan and New Guinea to California and Central America. In the western part of this region, primarily in the littoral zone, 5 million tons of fish, invertebrates and algae are taken, over 8% of the total world production. A tremendous assortment of animals and plants is taken here, including Sciaenidae (large and small yellow perch), anchovies, Scombridae, Carangidae, Thunnidae, Clupeidae, Euselachiae, rays and other fish, as well as squid, octopuses, cuttlefish, bivalves and Gastropod mollusks, shrimp, lobsters, crabs, sea urchins, Holothurioidae and other invertebrates, the share of which, for example in the Japanese catch, is as high as 30%. Furthermore, large quantities of bivalve mollusks are raised off the coast of Japan, then used as food and for the production of pearls, and as much as 500,000 tons of seaweed is raised as food.

The high biologic productivity and utilization of the most varied representatives of marine fauna and flora have led to the fact that the total fish production on the shelf along the east coast of Japan is as high as 1,300-1,500 kg/km^2, in the pelagic zone--1,200-1,300 kg/km^2, i.e., significantly greater than the equivalent figures for most other regions of the World Ocean. Some increase in the volume of the catch here is possible, by intensification of the fishing of saury, horse mackerel, anchovies, small tuna and squid, and also by organization of catching of myctophids.

In the east central Pacific, near California, Mexico and Central America, fishing is relatively little developed, not nearly corresponding to the resources of this region. Only about 1 million tons is taken from this region, primarily tuna, marlin, mackerel and some benthic species of fish, the production per unit area being only about 20 kg/km^2. However, tremendous accumulations of anchovies have been found here, allowing a catch of over 1 million tons per year, as well as large populations of mackerel, squid, pelagic crabs and certain other organisms, organization of production of which could increase the catch in this region to at least $2.5\text{-}3.0 \cdot 10^6$ t.

South Pacific. The oceanographic mode, peculiarities of the composition of the commercial fauna and its distribution in the southeast Pacific are determined to a great extent by the influence of the cold Humboldt current and the Peruvian coastal upwelling. Here we find one of the most numerous fish populations in the World Ocean--The Peruvian anchovy, which has yielded in certain years, catches of as great as 11-13 million tons, i.e., up to 7,200 kg/km^2. This level of fish productivity is the highest in the World Ocean. In addition to the anchovies, the pelagic zone is inhabited by tuna, marlin, sauries and squid. Within the limits of the narrow continental shelf are many hake, horse mackerel and mackerel, fishing for which could yield over 1 million tons.

The Southwest Pacific is somewhat different, being populated by such species as sardines, Beryciformes, poutassou, plaice, etc., which make up over half of the still small catch of the region ($0.4 \cdot 10^6$ t). The production here is as yet the least of all regions of the Pacific ocean--only 12 kg/km^2. Doubtless, the development of fishing in this region, the resources of which are still negligibly used, will allow an increase in the total catch to at least 2 million tons, increasing the useful fish productivity by many times.

The southernmost regions of the Pacific are in the Antarctic. Here, great resources of Antarctic krill, Serebryanka, etc. wait to be used.

Indian Ocean. Here, only $2.7\text{-}3.0 \cdot 10^6$ t of seafood is caught, 35-40 kg/km^2 for the entire ocean. This is significantly less than the other ocean basins. Doubtless, one reason is the insufficiently developed fishing industry, particularly of pelagic fish, but it is thought by most researchers that even significant intensification of fishing, bring the catch up to the maximum possible level of 5-6 million tons, would not increase the fish productivity of the shelf to over 350 kg/km^2, of the coastal pelagic zone to over 250 kg/km^2. The most productive regions are the coastal zones of the northwestern portion of the ocean, particularly the Gulf of Aden and Bay of Bengal, the waters of the east African coast, the regions of Madagascar and the Seychelles Islands, as well as the open regions of the ocean in the areas where masses of water of different origins come into mingle.

Species fished for here include sardines, large and small tuna, mackerel, sharks, as well as Sciaenidae, Lucyanidae and other benthic fish. There are many squids and lobsters (off the coast of Africa), shrimp and other commercial invertebrates. In the regions around the subantarctic, there are several species of fish (nototheniids, etc.) which may be of limited significance. Further development of fishing should primarily follow the path of utilization of the fish resources of the pelagic zone, particularly the sardines, mackerel, small tuna, squid, etc., and also organization of fishing for bottom-dwelling fish off the west coast of Australia and the east coast of Africa.

To complete our review of the distribution of oceanic commercial biologic resources, we should emphasize once more that fishing industry studies of the World Ocean indicate that there is a genuine possibility of significantly increasing the current catch of ocean fish and large invertebrates. Catches can be increased to the greatest extent in the Atlantic (by 10-12 million tons) and Pacific (by 12-14 million tons) basins. The greatest portion of the probable increase (21 million tons--87%) will be accounted for by inhabitants of the pelagic zone.

Marine mammals (whales and seals) can provide no increase in the current catch level, and for the next few years, hunting of these mammals will continue to decrease.

1.4 Basic Trends in Further Development of Ocean Fishing

The study of the processes of biological productivity occurring in relatively small seas (the Azov Sea, Caspian Sea, Black Sea, Baltic Sea and North Sea) have shown that the total production of fish (expressed as weight) is usually 50-100 times less than the annual production of invertebrate, plankton and benthos. The production of the most valuable species from the standpoint of food--the tuna, marlin, mackerel, sailfish, etc., as well as the sharks--which occupy the fourth, fifth or even sixth trophic levels, are hundreds or thousands of times less than the production of phytophagous and planktonophagous fish. Thus, based on the primary production of the ocean, as a result of the tremendous losses in the intermediate links of the food chain, only a relatively small quantity of fish production needed for man is created. This type of loss occurs, in particular, due to the great number of "food deadends." For example, in the North Sea, over 90% of all of the edible animals are consumed without any benefit from the standpoint of commercially valuable animals.

The predominant portion (75%) of Black Sea zooplankton consists of predators--Sagittae, Ctenophora, Noctiluca, which are almost never used as food by fish, but they consume tremendous quantities of edible zooplankton. Losses of this kind are found in the other regions of the ocean, as well. At best, 30% of the total biomass of the zoobenthos from the continental shelf of the World Ocean may be used as food by fish and other commercial species, while the remainder are terminal links in food chains. Unless a transition is made to commercial utilization of species at lower trophic levels and significant adjustments are made to the biologic production processes, we cannot expect any significant increase in the world catch. One means for increasing the volume of oceanic biologic resources usable by man might be the organization of fishing for the massive representatives of zooplankton. However, in addition to the undoubtable successes, the first steps in this direction will also involve many difficulties.

Various means and methods of expediently changing individual links in the oceanic processes of biologic production, making them yield higher results from the point of view of man, could be of great significance. Various forms of biologic reclamation, acclimatization and transplantation of commercial and feed organisms, the creation of new hybrid forms for stocking of regions with a good food base, but environmental conditions which are unfavorable for the ordinary species, incubation and raising of larvae and fry of certain commercial fish, to be subsequently released in the sea, the creation of "underwater gardens" and marine fish farms, alteration of the oceanographic modes of individual regions in the seas and oceans by means of hydraulic structures, and many other methods should be studied and, possibly, may be found to be effective for these purposes.

A decrease in the quantity of harmful animals by technical, biologic, chemical or other methods would allow the food resources available to commercial species to be increased by many times, thereby facilitating an increase in their population and production. Purposeful catching of predators might significantly increase the catch of more peaceful fish. Specialized intensive fishing for a single species (at times, even a species with no great food value) might open the way for an increase in the population for another species, the catch of which we would like to increase. The current scales of commercial effort and the nature of equipment used for fishing can allow almost complete elimination of a population. Transplantation of juveniles of commercial species to more favorable areas for their further growth can improve the utilization of the food base and yield thousands of tons of additional fish production. Acclimatization of food and commercial species also promises to be one method of improving the qualitative composition of the fauna and increasing the fish productivity of the ocean. Large areas of the shelf regions of the Barents Sea, Bering Sea, Sea of Okhotsk and other seas are covered throughout the year by waters of low temperature, and are far from the wintering areas of commercial species. They contain over 100 million tons of edible benthos, practically unutilized by fish. Transplantation of cold-loving benthophagous fish into these areas might lead to the inclusion of another, significant food base in the process of creation of fish production. The great successes of marine "fish husbandry" indicate that the future for underwater farms, breeding species utilizing the natural food base, is quite promising.

We should emphasize once more the special significance of the creation of truly efficient oceanic fish farming for the most effective utilization of the biologic resources of the ocean and achievement of the maximum, most stable catch. It should be recalled that the fishing conducted to date in the World Ocean is far from efficient. We are seeing cases at the present, for example, of significant changes in the age composition of stocks under the influence of fishing, leading to a reduction in the area of distribution, underutilization of the food base and, thereby, significant reduction in reserves. This is particularly true of cod in the Arctic-Norwegian area, Atlantic and Pacific sea perch and many other species. The sharp decline in the population of whales in the Antarctic has led to underutilization of their food resources (krill). Naturally, before we take steps to improve the biologic processes in the ocean, we must develop a plan for efficient utilization of the biologic resources available with particular caution, carefully considering the peculiarities of these processes.

All of this requires expansion and deepening of our knowledge concerning the regularities controlling these processes, the primary links in the food chain, leading to the final goal--fish productivity, the energy balance and energy losses during development of biologic processes and transformation of energy, etc.

The period of prospecting and study of the biologic resources of the World Ocean is now coming to an end; the time has come to begin the period of creation of oceanic fish farming; the problem of controlling the biologic processes occurring in the ocean demands solution.

The basic means and methods for further significant increases in the volume of the seafood catch from the World Ocean are beginning to be seen; successful employment of these means and methods would allow the total catch to be at least doubled in the next 20-30 year.

The biologic resources of the World Ocean can and should become the primary source for satisfying the ever increasing demands of man for aquatic animals and plants. However, this can be achieved only by radical alteration of man's attitude toward utilization of the riches of the sea. In addition to preservation and significant improvement of traditional fishing, and its transition to a more scientifically founded, efficient basis, allowing an increase in the present catch to 30-35 million tons and providing some stability for the fishing industry, the most important methods for future and even greater increases in total catch must be large-scale development of fishing for objects at lower trophic levels (particularly krill) and the expenditure of significant efforts toward the creation of farms for the growth of aquatic species.

Only by going over to highly productive fish farming in the seas and oceans, by raising algae, invertebrates, fish, and by actively increasing the biologic productivity of natural communities, can man fully utilize the tremendous potential resources of the World Ocean.

2. Introduction and Acclimatization of Marine Organisms

(T. S. Rass, O. G. Reznichenko)

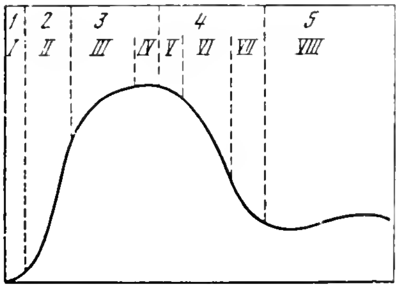
The composition of the fauna and flora of the oceans and seas is related to a great extent to the history of their formation. Many regions of the World Ocean are exposed to similar climatic conditions, but are separated by barriers which are impassable to hydrobionts. The fauna and flora of these regions contain taxonomically different, but ecologically similar components, based on vicarious species.

Over the past centuries, and particularly the 20th century, stable species compositions and relationships of components of biota in many regions have been disrupted by the introduction (stocking) and acclimatization of exotic (foreign) species; we shall refer to these species as exota. The spreading of many species beyond the limits of their ordinary area of distribution occurs constantly, in spite of the impediments (in the words of L. A. Zenkevitch), i.e., impassable natural barriers. The most important means by which hydrobionts are carried from one body of water to another is man. Independently of the wishes of man, many species expand their area of development, utilizing anthropogenic changes in nature: the digging of canals, changes in estuarine spaces of seas due to decreases and alterations of runoff resulting from the diversion of water for irrigation, the construction of dams, the descent of industrial and domestic wastes down rivers, the dumping of heated water by shoreline power plants. To a still greater extent, the spreading of exota has been facilitated by transportation. This is clearly indicated by the fact that, due to the recent spreading of certain invertebrates carried by ships (the crabs *Eriocheir sinensis*, *Rhithropnopeus harrisi tridentatus*, *carcinus maenas*, the cirripedia *Elminius modestus*, *Balanus improvisus*, *B. eburneus*, the polychaeta *Mercierella enigmatica*), the total area of their potential distribution has now reached $2.5 \cdot 10^6$ km^2, equal to the total surface of the Barents Sea, the Baltic Sea, the White Sea and all of the southern seas of the USSR (Reznichenko, 1976). The naturalization of such autoimmigrants is greatly facilitated by underwater substrates created by man. Their total surface is now at least 2,000 km^2 (Reznichenko, 1976). Finally, man actively distributes organisms for their maintenance in aquariums (from which they frequently enter natural bodies of water) and for acclimatization, breeding and culturation in new regions.

In connection with the improvement of transportation, the possibilities of introduction and acclimatization of marine exota have greatly increased and have become at the present time an important problem for oceanography. Until quite recently, even the most complete reviews of oceanography did not even touch on this problem; now, that would be a clear omission.

2.1 Factors and Phases of Acclimatization

The possibility of entry of a foreign organism into the composition of biota formerly foreign to it results from two factors--endogenous and exogenous. The endogenous factor is the genuine capability of the incoming organism to exist in the new body of water, determined by the agreement of the abiotic characteristics of the body of water with those required by the exota. Of decisive significance is the presence of conditions necessary for the most labile period of the life cycle: spawning and the initial stages of development. The exogenous factor is the possibility of a species occupying an ecologic niche in a new body of water by expelling a local species with an analogous ecologic profile, or by moving into an unoccupied ecologic niche which corresponds to the ecologic valence of the intruder. Obviously, in addition to endogenous (essentially autoecologic) and exogenous (synecologic) factors, the geographic factor is also important: the total correspondences of the conditions in the recipient water to the conditions in the donor body of water, or the primary area of distribution.



Phases of acclimatization during introduction of a hydrobiont into a new body of water (according to Zinkevitch, 1940, altered): I-VIII, Phases of acclimatization; 1-5, Periods of acclimatization.

Anthropogenic transplantation and introduction of exota into new bodies of water is performed by man either intentionally (transplantation) or when these organisms use human transportation equipment without human intention (autotransplantation). During acclimatization in the recipient body of water, in most cases the exota encounter significant resistance from the local biota, or insufficient agreement of abiotic conditions to the specific conditions necessary for life of the transplanted species.

In case of successful introduction of an intruding organism, eight phases of acclimatization occur (Zenkevitch, 1940). After the first phase of barely noticed appearance (due to the small population) of the intruder, there is usually a phase of rapid multiplication, a result of the fact that the intruding species has no natural enemies or serious competitors in the new body of water, providing the quantity of food is sufficient. In certain cases, the rate of this initial development may be compared to an ecologic explosion (Elton, 1960). As a result of the massive increase in the population of the intruding species, saturation of the new area occurs, the breeding rate of the intruder decreases (Phase III of acclimatization). For some time the population of this species remains at the same high level (IV). Then, a phase of slight (V), and then more rapid (VI) population decrease occurs, due to the appearance of competitors and natural enemies and a reduction of the available natural food. Subsequently, the rate of decline slows (VII), and, finally, the population of the species reaches a certain steady level, subject to the fluctuations which are normal for all species (Phase VIII). This detailed system of L. A. Zenkevitch, which reflects the process of acclimatization quite well, can be reduced to five main periods (see figure): I--the initial phase--the moment of introduction (Phase I), 2--the increase in population or intensity of intrusion (Phase II), 3--the period of high population (Phases III-IV), 4--the period of decreasing population (Phases V-VII), and 5--the period of naturalization of the introduced species and the stabilization of its population (Phase VIII).

2.2 Forms of Acclimatization

Acclimatization of exota can significantly influence the composition and productivity of the biota of the recipient body of water. The hydrobionts introduced frequently replace or reduce the population of local forms. The introduction of the Indian-Western Pacific diatom Biddulfia sinensis, carried by the hulls of ships, into the North Sea around 1903, led to its colossal multiplication, and in some parts of the sea it became the dominant species of phytoplankton (Hardy, 1956). A gastropod mollusk Crepidula fornicata was unintentionally carried from the east coast of North America to the coastal waters of western Europe, where it spread from Sweden to France (Walne, 1956; Walford, Wicklund, 1973) and became a very numerous species on the oyster bars, causing significant deterioration in the conditions of existence of oysters and requiring that the oyster bars be cleared with special dredges. The boring mollusk Ocenebra japonica, unintentionally introduced along with the Pacific oysters brought in from Japan, has done great harm to oysters along the west coast of North America. Similar occurrences have been reported in the Black Sea, where the predaceous mollusk Rapana venosa, accidentally brought in from the Sea of Japan, has acclimatized and has virtually wiped out all of the oyster bars in the eastern portion of the sea in a few years, greatly reducing the biomass of other large bivalve mollusks.

We must distinguish substitution acclimatization, such as the cases we have just described, from interstitial acclimatization (a term used by Zenkevitch, 1963), when the new species inserts itself into the composition of biota without any apparent expulsion of any aboriginal species. Examples of interstitial acclimatiztion are rather obvious in cases of intrusion of species which differ in terms of ecology from the components of the biota of the recipient body of water. For example, the planned introduction of the polychaete worm Nereis diversicolor, the bivalve mollusk Abra (=Syndesmya) ovata and the mullets Liza (=Mugil) aurata and L. saliens from the Azov Sea to the Caspian Sea in 1938-1947 has led to a significant increase in the biomass of the benthos of the Caspian Sea and to the formation of a Caspian population of mullets, apparently nearly as numerous as the initial population. In this case, expulsion of local forms was not observed, and the acclimatization was doubtless useful from the practical point of view. A similar result was obtained by the carefully planned and well-founded introduction of certain reef and estuarine species of fish and invertebrates to the Hawaiian Islands. The Hawaiian Islands are poor in natural fauna, as is the usual case for isolated islands, the local fauna consisting mainly of species which have a long larval period, so that larvae can be carried in by currents from the life-rich regions of the tropical western Pacific. The islands had no representatives of the species-rich genera of fish Lutianus and Lethrinus, had only 2 species of groupers (Epinephelus) and 2 species of the Clupeid group of sardines, of which other islands in Oceania had from 8 to 22 species. The mollusks and crustacean fauna were similarly poor. As a result of transplantation from the waters of the Atlantic states of America, the islands of central Oceania, Japan and Southeast Asia, the marine fauna of the Hawaiian Islands was enriched with useful mollusks, crustaceans and fish, which acclimatized with no noticeable harm to the local biota (Table 20).

The relative level of saturation of biota is of great significance for the introduction and acclimatization of exota, since it defines to a great extent the possible direction of introduction and form of acclimatization. This is well illustrated by comparison of the fauna of bodies of water which are more or less similar in their physical and geographic conditions but differ in terms of saturation of biota.

For example, joining of the Mediterranean and Red Seas through the Suez Canal in 1869 opened a path for the fauna of these bodies of water through what had been an impassable barrier. There are difficulties in this method--highly saline water areas (Great Salt Lake, etc.). Nevertheless, some 130 species from various systematic groups of benthos and nekton have succeeded in using such opportunities to introduce themselves into new bodies of water. Eighty-five species of invertebrates and 25 species of fish from the Red Sea have settled in the Mediterranean, while 6 species of invertebrates and 7 of fish from the Mediterranean have settled in the Red Sea (Table 21). The difference in the number of fish moving in the two directions has resulted from the fact that the fauna of the Mediterranean Sea represents significantly fewer species than the Indian-Western Pacific Ocean fauna. For example, in the Mediterranean we find no species of a number of characteristic Pacific families: Dussumieridae (2 species have settled in the Mediterranean), Platycephalidae (1), Siganidae (2), Leiognathidae (1 species).

2.3 Transoceanic and Inter-oceanic Transplantation

The global scale which has been achieved by transplantation and introduction of marine organisms is illustrated by examples of both autotransplantation and of transplantation. Long-range autotransplantation of invertebrates is clearly seen in examples of transplantation by ships, on their hulls or in ballast water (Bishop, 1951; Walford, Wicklund, 1973; Hoese, 1973, et al.). We can present

Table 20. Successful acclimatization of marine commercial species of fish and invertebrates in the waters of the Hawaiian Islands (Walford, Wicklund, 1973).

Species	Origin	Date of Transplantation	Results
Bivalve Mollusks			
Tapes philippinarum	Japan	1920	Numerous, utilized.
Citherea meretrix	"	1926, 1939	Well acclimatized.
Crassostrea virginica	Atlantic coast of USA	1871 and 1883, unsuccessful 1893 and 1895, successful	Common on the rocky littoral of Kaneoha Bay.
Crustaceans			
Scylla serrata	Samoa	1926-1935	Common on all islands, valuable food product.
Fish			
Marquesas sardine *Herclotsichthys vittatus*	Marquesas	1955-1957	Well acclimatized.
Cephalopholis argus	Society Islands	1956	Acclimatized and fished.
Lutianus kasmira	Marquesas	1958	Rather common, commercial since 1962.
L. vaigiensis	Marquesas Society Islands	1955-1958	Common, fished since 1969.
Mollienesia latipinna	Texas	1950	Brought in to destroy mosquito larvae. Adapted well to salty water.
Tilapia mossambica	Singapore	1951	Well acclimatized to brackish and fresh water.

Table 21. Autointroduction from the Suez Canal of various hydrobionts (according to Walford and Wicklund, 1973).

Group	Number of Species	
	Passing from Red Sea to Mediterranean	From Mediterranean to Red Sea
Algae	1	2
Sponges	2	3
Coelenterata	29	-
Worms (Polychaeta, Sipunculoida)	10	2
Crustacea	14	1
Pantopoda	1	-
Molluska	20	-
Echinodermata	3	-
Ascidia	6	-
Fish	25	7
Total	111	16

examples of transplantation of 5 species of the Cirripedia crustaceans, the Balanidae, attached to the hulls of ships: from Australia to the waters of western Europe (*Elminius modestus*, about 1940); from the coast of America to the coast of Europe, southern Australia and Japan (*Balanus improvisus*, late 19th and early 20th centuries); from the Atlantic coast of America to Europe, then later to Japan (*B. algicola*); from the tropical Pacific to Japan and California (*B. amphitrite*, about 1940 and later). Autotransplantation of other invertebrates overgrowing the hulls of ships has occurred over equally long distances: the polychaete *Hydroides norvegica*, the Bryozoa *Bugula flagellata*, the hydroid *Bougainvillia ramosa*--from the North Atlantic to Australia and New Zealand; the polychaete *Mercierella enigmatica*--from India to western Europe and the Caspian, the Bryozoa *Victorella pavida*--in the reverse direction. Ships have also carried many other species across oceans which have acclimatized in new regions: the mussels *Mytilus edulis*--from Europe to Japan, the North Atlantic *Mya arenaria* to the Pacific waters of America and to the Black Sea, the *Rapana venosa* from the Sea of Japan to the Black Sea, the crabs *Callinectes sapidus* and *Rhithropanopeus harrisii tridentatus* from the waters of eastern North America to the seas of Europe, and the last-named species also into the Caspian Sea and the Pacific waters of America; the European *Carcinus maenas*--to the Atlantic waters of America; the East Asian *Eriocheir sinensis*--to the waters of western Europe. Cases are known of transoceanic autotransplantation of fish--small bullheads, blennies, etc.--in the ballast water of ships, during transportation of dry docks, shipping of large mollusks, etc.

Acclimatization by means of planned or sporadic transoceanic shipment has been performed on a particularly large scale for oysters and fish. At various times, 7 species of oysters have been transplanted. Successful transoceanic naturalization has been achieved for only some of them. For example, the European oyster *Ostrea edulis* has been acclimatized off the Atlantic coast of America, off the shores of South Africa and in Japan. The Virgin Islands oyster *Crassostrea virginica* has been naturalized along the Pacific coast of America and in Hawaii, where it was taken from California. The Pacific oyster *C. gigas* has been acclimatized along the east coast of America, in Hawaii, France, Australia and New Zealand. As concerns the remaining species of oysters, their introduction in regions not as far from their natural area of distribution has been partially successful. The practical significance of the acclimatized oysters has been very great: the oysters acclimatized in new regions have yielded significant production. For example, the annual production of the far-eastern oyster in the western waters of America is $30\text{-}40 \cdot 10^3$ t.

Transoceanic introduction and acclimatization of marine commercial fish is, actually, of significant practical interest. These operations have been performed, however, primarily with transitional (anadromous) and semitransitional species, and only to a smaller extent with true sea fish. One significant achievement has been the introduction of the anadromous *Alosa sapidisima* from the Atlantic coast of America to the waters of the Pacific coast, achieved by the transportation of developing eggs in 1871-1886. This shad was naturalized in 1873, and by 1886 had become one of the most numerous commercial fish in California. It extended to the north and south from its point of introduction, occupying an area of distribution from Mexico to Alaska (a few even reaching northeast Asia). The greatest catch, about 3,000 tons, was achieved in 1914, after which the catch decreased to 300-1,000 tons per year (Mansueti, Colb, 1953; Walford, Wicklund, 1973).

In 1879 and 1882, fry of the semitransient *Roccus saxatilis* (frequently improperly called striped perch) was transported from the Atlantic coast of the USA and released in San Francisco Bay. This fish was naturalized in the waters of the Pacific, occupying an area of distribution from British Columbia to southern California and yielding commercial catches of up to 500 tons per year (Raney, 1952).

Beginning in 1872, many attempts have been made at transoceanic transplantation of salmon, particularly species of the Pacific genus *Oncorhynchus*. Attempts have been made to introduce Pacific salmon to various regions of the Atlantic Ocean, from Canada to Florida and from Norway to Italy, in Mexico, Nicaragua, Hawaii, Argentina, Chile, Australia and New Zealand (Davidson, Hutchinson, 1938). The Pacific salmon have acclimatized (Stokell, 1955; Rodway, 1957) in a few regions of northeast America (silver and humpback salmon in the rivers of the Gulf of Maine, New Brunswick and Ontario), in Chile (silver salmon, blue-back salmon), and the south island of New Zealand (king salmon, blue-back salmon). However, the populations formed in the regions have frequently gone over from an anadromous to a river mode of life, as a result of which their population has been greatly reduced (Stokell, result of which their population has been greatly reduced (Stokell, 1961) or even completely eliminated (in the Gulf of Maine). In 1933-1939, in the Soviet Union, dog salmon were introduced to the rivers of the White and Barents Seas, but this experiment was not successful. In 1956-1964, each year, developing eggs of humpback salmon, and, in smaller quantities, dog salmon, were transported from Sakhalin to Murman and the White Sea, where the eggs were reincubated, the larvae and fry were released into the sea. In all, some 49 million individuals were released. In 1960, humpback salmon, apparently some of those fry released in 1959, returned to the coast of the White Sea, Murman, as well as Norway, England, and Iceland; in all, over 80,000 individuals were counted (Shearer, 1961). Later, great runs of humpback salmon were reported in 1965, 1971 and 1973, while in the other years, the runs were much smaller--a few dozen to a few thousand fish. Since 1966, stocking of fry has been resumed. Apparently, complete naturalization of the humpback salmon to the European north has not occurred, and its existence there is supported by the transport of eggs from Sakhalin and maintained by the fortune of favorable weather conditions (mild winters) in some years.

Transplantation of commercial sea fish in the Pacific Ocean basin has involved as yet only a few species. The natural area of distribution of the valuable milkfish (Chanos chanos) a hundred years ago encompassed the indo-west Pacific and extended from the Red Sea and east Africa to Hawaii and Polynesia. In 1876-1877, a small number of chanos larvae was released in the sea near San Francisco (H. M. Smith, 1896). Finding a free ecologic niche and favorable conditions there, the chanos was fully naturalized and spread south--into the Gulf of California (McHugh, Fitch, 1951) and along the coast of Central America to Panama. At the present time, the milkfish is one of the commercial species of fish along the Pacific coast of Mexico (Berdegue, 1956; Schuster, 1960; Lachner et al., 1970). The successful introduction of 4 species of sea fish from the Society Islands and the Marquesas to the waters of Hawaii was described earlier. We should also recall the successful acclimatization of the salt-water tilapia (Tilapia mossambica) to estuaries, after it was transported to Honolulu from Singapore in 1951.

The introduction of 2 species of mullet from the Black Sea into the Caspian Sea was quite successful. The prospects for the introduction of the temperate and cold-water far eastern Kamchatka mackerel (Pleurogrammus monopterygius) into the Barents Sea are quite good. A small number of developing mackerel eggs was successfully transplanted to eastern Murman in 1958, 1971-1972 and 1976, where they incubated and the viable larvae were released into the sea (Rass, 1962, 1965). This work has, unfortunately, remained uncompleted.

The transplantation of organisms desirable to man is, in many cases, accompanied by unintentional autointroduction of undesirable animals, due to insufficient caution in the selection of materials.

2.4 Parameters of Introduction and Acclimatization of Exota.

The actual possibility of introduction and acclimatization (naturalization) of exota is determined by the physical-geographic, autoecologicand synecologic, or biotic parameters. The possibility of acclimatization is determined primarily by the agreement of the physical-geographic (abiotic) conditions of the acceptor body of water with the conditions in the donor body of water. The basis of this agreement in naturally separated regions is the symmetry of the ocean (Zenkevitch, 1948). Regions of the oceans which are located in areas of similar climate but are separated by impassable continents, climatic or water barriers, may be quite similar in terms of abiotic conditions. The regions of the Boreal labitudes of the Atlantic and Pacific Oceans, the western and eastern waters of these oceans, the Boreal and Notal regions, the Arctic and Antarctic, as well as the tropical areas of the Atlantic, Indian and Pacific Oceans are comparable in this aspect. The capability for acclimatization and naturalization is determined by the autoecologic parameters when the acceptor body of water has the conditions necessary to the intruder species during the period of reproduction for survival of the eggs and larvae, which are more vulnerable than the species in other periods of life. The possibility of introducing exota is determined by synecologic parameters, depending on the local biota, the existence of an ecologic niche which is open, or occupied by a less viable local species, the presence of sufficient food resources, the resistence of the intruder in terms of parasitic invasion and its susceptibility to local predators. These parameters basically determine the nature of acclimatization, either interstitial or replacement (Zinkevitch, 1963).

The presence of an unoccupied niche in the biota of individual regions of the ocean is determined by the geologic history of the fauna and flora. Quite demonstrative in this respect, for example, are the unoccupied or weakly occupied niches of the southern Boreal transitional fish off the Pacific coast of North America (in comparison to the Atlantic coast), the niche of silt-feeders in the Caspian (in comparison to the Azov Sea), the niche of temperate and cold-water fish in the Barents Sea (in comparison to the Bering Sea), the niches of a number of tropical species in Hawaii and the eastern Mediterranean, of brackish-water hydrobionts in the Caspian Sea, Boreal fish in the cool layer of water at 50-100 m depth in the Black Sea (in comparison to the Baltic Sea), the niche of the tropical phytoplanktophages in the Caribbean Sea (in comparison to the South China Sea and, after acclimatization of the chanos, to the Pacific waters of Mexico), the niche of large benthophages in the Arctic (in comparison to the Antarctic), etc. These niches are easily filled by immigrants from more life-saturated regions, or may be filled by introduction of the corresponding species (Rass, 1965, 1975).

Unoccupied niches in the seas are also created as a result of human activity, which may change the environment and the composition of biota by changing the mode of continental runoff, resulting in a decrease in the population of transitional fish, or by extremely selective fishing for certain fish, as well as development of their competitors. The niches thus liberated can be filled, for example, in our own southern seas, by the introduction of sea fish: the Baltic herring and the Black Sea anchovy and garfish to the Caspian Sea, the Japanese pike-perch to the Black Sea (Rass, 1965, 1975). The unoccupied niches are easily filled by autointroduction of undesirable, useless or even harmful species, utilizing human technology. Therefore, it is important not to delay introduction, efficient transplantation and acclimatization of desirable commercial and food organisms needed by man.

CHAPTER II. EFFECT OF OCEAN POLLUTION ON MARINE ORGANISMS AND COMMUNITIES

1. Chemical Pollution and Its Effect on Hydrobionts.

(S. A. Patin)

The effect of man on the living resources of the biosphere, including the World Ocean, is not limited to simple extraction of biologic production, cultivation and alteration of the composition and structure of populations. Over the last few decades, the influence of industrialization and urbanization of modern society, intensification and increased use of chemicals in agriculture and other attributes of scientific and technical progress have particularly rapidly grown and expanded, resulting in pollution of the biosphere and the appearance of new ecologic factors. The environment is being transformed to a qualitatively new state, which is sometimes referred to as the "biotechnosphere" (Khil'mi, 1975).

The pollution of the World Ocean occupies a special place in the framework of this complex and multifaceted problem. Many, if not most, of the toxic substances liberated by man on land enter the ocean, creating situations of local, regional or global pollution of the seas and oceans. Due to the unity of the structure of the ocean, regional anomalies are reflected in the status of neighboring regions and of the entire system as a whole.

As a result of pollution, the distribution of certain artificial substances has become planetary. The material chemical composition of the marine environment, formed over the duration of a number of geologic eras, to which the animal and plant life of the seas and oceans has adapted by evolution, is undergoing noticeable, at times significant, changes in the space of decades. The biologic consequences of this process, involving the formation of a new quality of the marine environment, cannot but attract the attention of modern science and must be the subject of comprehensive study in many nations of the world. The status and results of this type of work go far toward determining the nature, scale and effectiveness of national and international efforts to protect the seas and oceans from pollution.

1.1 Status and Methodology of Investigations.

We can distinguish three main trends in the overall system of ecologic studies on the problem of pollution of the World Ocean:

- Pollution monitoring--a system of observation, testing, estimation and prediction of the quality of marine environment;

- Biogeochemistry of pollutants--the study of the elements of balance, processes of biologic concentration and transport through the food chain, biogenic migration and transformation of artificial substances in marine communities and ecosystems;

- Ecologic toxicology--the study of the effects of toxic factors on the hydrobionts and communities, estimation of the biologic and ecologic consequences of the pollution of the marine environment, regulation of permissible norms for the content of toxic substances.

The level of development of the basic principles and methodology of studies in each of these three areas differs significantly. Studies of situations of pollution of individual marine regions are most advanced. This has been facilitated by the successes achieved in processing large volumes of information and the progress in the area of analytic methods of detection and recording of trace quantities of man-made substances in natural environments and substrates. The methodologic principles of large-scale monitoring are being intensively developed in our country and abroad, and also by means of international cooperation (Goldberg, 1970; Marine Environmental Quality, 1971).

The situation is quite different in the area of marine biogeochemistry of toxicants and ecologic toxicology. In spite of the abundance of the works dedicated to various aspects of the interaction of marine organisms and communities with toxic man-made components of the environment, the general methodology of studies of this nature, the foundation of areas for study and summarization of the available materials are essentially in the earliest stages of development. This is particularly true of marine ecotoxicology--a new area of ecologic investigation at the junction of marine biology, toxicology and experimental ecology.

It should be noted that marine ecotoxicology and the biogeochemistry of pollutants mutually supplement each other, studying two aspects of a single process of interaction between marine organisms and the anthropogenically altered toxic environment. The situation is somewhat similar in the area of study of radioecologic phenomena in the ocean (Polikarpov, 1964).

In terms of methodology, it is important to emphasize that ecologic-toxicologic studies should be directed toward the study of anomalies in marine communities and ecosystems under conditions as close to natural conditions as possible. Studies performed directly in polluted regions are ideal from this standpoint (Bechtel, Copeland, 1970; Bellan, Bellan-Santini, 1972; Mironov, 1972; Nelson-Smith, 1973); however, they are possible only in cases of actual severe pollution, when the biologic effects are obvious and can be directly quantitatively measured. It is much more difficult to evaluate the actual or potentially possible results under conditions of low levels of chemical pollution. In these situations, the methods of experimental ecology, toxicology of representative species and communities of marine organisms, estimation of their production in situ in the presence of toxicants, experimental modelling of food chains and ecosystems, and a number of other methodologic approaches must be used (Patin, 1971; Fontaine, 1972; Aubert, 1973; Patin et al., 1975).

1.2 Basic Features and Trends in Pollution of Ecologic Zones of the World Ocean.

The flow of publications on the problem of chemical pollution of the marine environment and hydrobionts in recent years has greatly expanded and amounts to some thousands of articles; however, summary works are rare (Goldberg, 1970; Marine Environmental Quality, 1971; Mironov, 1972; Aubert, 1973; Nelson-Smith, 1973; Loranskiy et al., 1975). In particular, we know of no description of the most general regularities of the process of pollution of the seas and oceans in relationship to the specifics of the biologic structure and biologic production in the World Ocean.

One interesting but as yet unrealized approach to the analysis of the large-scale picture of distribution of man-made chemical products in the ocean is the utilization of the extensive materials available on the behavior and transfer of artificial radionuclides in the biosphere. If we consider that the large-scale (background) pollution of the biosphere is determined primarily by atmospheric transfer and fall-out of pollutants from the atmosphere, it is difficult to find any other precedent involving large-scale pollution of the biosphere in which these processes would be more clearly and obviously reflected than in the cases of distribution of the products of nuclear testing. The great magnitude, scale and variety of studies on this problem, including studies concerning artificial radioactivity of the marine environment and organisms, are also without precedent.

The existence of an atmospheric reservoir for the primary groups of chemical toxicants and the magnitudes of the flows of these toxicants into the World Ocean can be judged from the information presented in Table 1, from which we can see that, with the exception of crude oil, all of the polluting substances enter the World Ocean to a great extent through the atmosphere.

Each year, some $8 \cdot 10^9$ t of fossil fuel is burned in the world, and over 10^9 t of solid, vapor and gaseous compounds are emitted into the atmosphere (Styrikovich, 1975). The existence of large-sale atmospheric transfer of man-made substances from the land into the ocean is indicated by the discovery of ash particles in the bottom sediment of the open ocean and the accumulation of heavy metals in the glaciers of Greenland (Bertine, Goldberg, 1971).

Atmospheric aerosols and fall-out over the ocean have been found to contain significant quantities of such products as DDT, polychlorinated biphenyls, mercury, lead, ash, in particles on the order of 1 μm in diameter, about the same size as the aerosol particles of radioactive fission products, meaning that they can be carried by the atmosphere over long distances from their source and can reach the upper layers of the atmosphere.

Table 1. Character of production and rates of delivery to the World Ocean of the primary groups of pollutants (marine environmental quality, 1971; Gesamp, 1974; Patin et al., 1974).

Substance	World Production t/yr	Entering Ocean, 10^3 t/yr		Atmospheric flux as a % of total amount entering ocean
		Direct pollution and runoff from land	Atmospheric flux	
Petroleum	$1.8 \cdot 10^9$	5,100	0	0
Hydrocarbons of petroleum origin*	?	?	90,000	95
Heavy metals				
Lead	$3 \cdot 10^6$	100	300	75
Mercury	$9 \cdot 10^3$	<3	18	>90
Cadmium	10^4	0.5	10	>90
Chlorinated hydrocarbons				
DDT	10^5	0.1	25	>90
Aldrin	10^5	<1	25	>90
Benzyl hexachloride	10^5	<1	50	>90
Polychlorinated biphenyls	$(5\text{-}10) \cdot 10^4$	<5	20	>90
Volatile organic compounds				
Dichloroethane	$5 \cdot 10^5$	?	500	?
Freons	$5 \cdot 10^5$	?	500	?
Others	$(2\text{-}3) \cdot 10^7$	?	3,000	?

*Gasoline, kerosene and other light fractions of petroleum, products of their incomplete combustion and degradation in the atmosphere.

In addition to the generally known groups of large-scale toxicants (petroleum and its products, heavy metals, chlorinated organic compounds), we should mention two more types of substances, the liberation of which into the environment is quite extensive. We are speaking of volatile organic liquids and gases (dichloroethane, freons, solvents) and carcinogenic substnces, which have blastomogenic properties (polycyclic aromatic hydrocarbons such as benzpyrene). information on the content of such substances in the sea and its orgnisms is as yet sparse; however, the scale of their production and entry into the environment is quite large: the annual rate of liberation of dichloroethane and freons into the atmosphere is at least 1 million tons, of volatile organic solvents up to 2 million tons (Marine Environmental Quality, 1971). The total quantity of persistent anthropogenic hydrocarbons (in addition to methane) entering the atmosphere is about 50 million tons per year (Duce et al., 1974). To this figure we must add the pollution of neritic marine waters and of the open ocean by solid wastes, consisting of various insoluble plastics and organic films, the world production of which is over 20 million tons per year (Marine Environmental Quality, 1971). A significant fraction of these products finally reaches the ocean. For example, the mean content of plastic particles in the Sargasso Sea is 290 g/km^2 (Carpenter, Smith, 1972).

We also must not forget the processes of eutrophication resulting from the liberation of organic substances, fertilizers, detergents and other compounds of phosphorus and nitrogen, leading to the intensive development of phytoplankton and certain species of benthic algae and, thus, to secondary pollution of the sea with the products of their metabolism and decay. However, these processes, like the processes of thermal pollution (see Chapter II, 3.), are generally localized in the neritic waters or internal bodies of water, and should not be considered to be a global situation.

Let us attempt briefly to describe the basic structural and dynamic peculiarities of the field of large-scale pollution of the ocean.

Increased pollution of the euphotic layer.--This distribution feature is rather obvious, since it is the surface waters which are the primary collectors of atmospheric pollution, littoral runoff, sewage and wastes of the most varied composition and origin. Depending on the rate of exchange and renewal of surface waters and, at times, on the rate of biosedimentation processes (Patin, 1970), a certain gradient of vertical distribution of pollution is created in the water; however, the levels of content of toxicants of all kinds generally reach their maximum in the surface layer.

Increased pollution of the neritic zone.--The available data on pollution of the seas and oceans indicate that there is a gradient of decreasing concentration upon transition from the neritic zone to the open ocean, resulting from the delivery of polluting substances into the sea from the land and their gradual dilution with increasing distance from the source, the localization of many types of human activity causing pollution (navigation, drilling for petroleum) in the shallower regions of the ocean, and the gradual purification of the air by fallout of aerosols as they move over the water body. Especially persistent fields of high levels of regional pollution are created in areas with limited water exchange, for example in the internal seas.

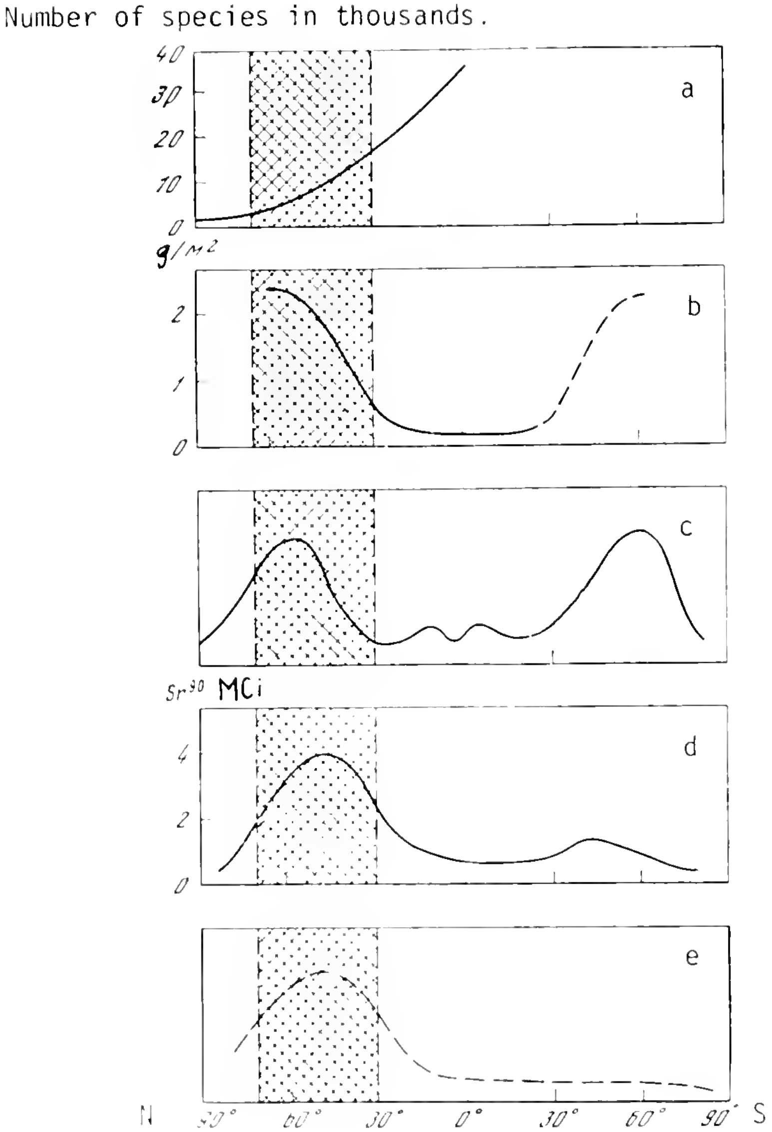
Zonality of distribution and the latitude effect.--As has been shown, using radioactive products as an example, finely dispersed aerosols are transferred and precipitate from the atmosphere in the zonal direction, forming latitudinal zones of intensive pollution at the parallels where the sources of atmospheric pollution are located (Karol', Malakhov, 1965; Nelepo, 1970). As a result, in the temperate latitudes of the northern, and to a lesser extent of the southern hemispheres, there are maxima of precipitation and pollution, while at the equator and in the polar regions there are minima. This global picture has been produced on the basis of observed data on the continental surface; however, there is every reason to extrapolate it to the World Ocean as well.

Atmospheric flux of chemical pollutants is primarily concentrated in the northern hemisphere, particularly at 30-70°N, where the main industrial zones are located and where most of the substances are produced which pollute the troposphere and subsequently precipitate into the ocean. According to some calculations, some 90% of all atmospheric pollution is accounted for by these regions (Duce et al., 1974). If we consider the zonality of the transfer of tropospheric aerosols noted above and the restriction of the maximum precipitation to the middle latitudes of the northern hemisphere, we can speak of the existence of a latitude effect in the large-scale distribution of chemical pollutants in the ocean with its maximum in the temperate latitudes of the northern hemisphere (see figure).

These considerations have been confirmed as yet only by the results of studies of artificial radioactivity (Popov, Patin, 1966), plus some information on chemical pollution of the waters of the North Atlantic (Simonov et al., 1974).

The mosaic nature of distribution.--Analysis of this phenomenon as applicable to artificial radionuclides has shown (Popov, Patin, 1966) that it cannot be explained by analytic errors in the determination of impurities in the sea water alone. This heterogeneity is characteristic for all trace elements in the marine medium, and its causes are probably related to the peculiarities of turbulent mixing of masses of water and the overall specifics of the behavior of trace quantities of substances in complex heterogeneous systems such as sea water. In this connection, we must recall the processes of sorption, hydrolysis and complex formation, which lead to the complicated and "anomalous" behavior of many trace impurities under conditions of great dilution in aqueous solutions.

Localization in the surface film.--This feature of the microstructure of the field of pollution is related to the physical-chemical and ecologic peculiarities of the thin surface film at the division boundary between the water and the atmosphere, where many



Zonality of distribution of certain biologic characteristics of the World Ocean and levels of pollution of surface (euphotic) layers of sea water. a--Number of species of marine animals (after L. A. Zenkevitch); b, c--Biomass of benthos and plankton (after B. G. Bogorov and L. A. Zenkevitch); d--Cumulative global store of strontium-90 (Patin, 1965); e--Hypothetical curve of variation in levels of chemical pollution. Shaded areas show position of latitude band of elevated pollution.

natural organic compounds with hydrophobic and surface-active properties are concentrated, creating a unique biotope of neustonic marine communities (Zaitsev, 1970). The known facts of localization of a number of toxicants in the surface film (Seba, Corcoran, 1969) have been confirmed by our own data (Table 2) obtained upon analysis by gas chromotography and atomic absorption of samples of sea water (film 60-100 μm thick).

Table 2. Distribution of certain ingredients between the surface film and sea water (Arcachon Bay, France, summer of 1973).

Ingredients	Mean concentration, μg/l In surface film 60-100 μm thick	 In upper level down to 50 cm	Coefficient of accumulation in surface film
Anionic detergents	850±75	10±1	85
DDT & DDD	95±10	0.10±0.02	950
DDE	86±9	0.10±0.02	860
Lindane	44±8	0.07±0.02	630
PCB	105±15	0.10±0.02	1,050
Hg	2,750±110	0.5±0.1	550
Pb	2,920±180	13.5±3.5	2,200
Cd	120±35	0.4±0.1	300
Cu	235±15	0.3±0.1	800
Zn	1,020±45	22±4	470

It must be recalled that the organisms of the hyponeuston include the stage of early ontogenesis of many hydrobionts, including commercial fish, and that this stage is most sensitive to toxic effects (Polikarpov, Zaitsev, 1969).

Superimposition of fields of pollutants and bioproductivity.--The general picture of the distribution of biologic productivity in the World Ocean can be characterized by concentration of living organisms in the surface layer and particularly in the neritic zone and the internal seas. It is in these zones also that the main fluxes and masses of all types of toxicants entering the marine environment are concentrated. Furthermore, the interfaces between the water and atmosphere, water and bottom, water and coast, river water and sea water, where complex physical, chemical and biologic processes occur, determining to a great extent the life of the ocean, are also areas of localization of higher concentrations of pollutants.

Relative stability of fluxes and levels of toxicity.--In contrast to the situation of strong but one-time local pollution, for example in case of an accident, when the toxicity of the environment, after reaching its maximum, gradually decreases, large-scale pollution not only does not decrease its intensity as long periods of time pass, but, in terms of a number of its indices, is gradually increasing. This is quite understandable if we consider the relative stability and the increasing trend of the characteristics of world industrial production, which correlate directly to the fluxes and levels of pollution of the hydrosphere.

1.3 Biologic and Ecologic Effects of Pollution.

The basic difficulty which arises upon analysis of the effects of anthropogenic changes in the chemical composition of the marine environment results from the fact that living systems react to the presence of toxic or other pollutant ingredients at the same time at all levels of organization of life--from the subcellular to the superorganismic. A complex mosaic of direct and indirect mechanisms and manifestations of the effects of toxicants arises, against the background of the natural dynamics of biologic processes.

Various versions of systematization of biologic effects and aftereffects of pollution of the marine environment are possible. In the first approximation, it is desirable to differentiate two groups of ecologic-toxicologic situations: direct toxic or stress effects on separate populations and communities, accompanied by rapid damage to the primary physiologic-biochemicl systems of organisms, with subsequent lethal intoxication, elimination of individual species or clear pathologic changes, and the effect of comparatively low concentrations of pollutants on the organisms and communities upon long-term, chronic pollution. The impressive, at times tragic, examples of situations of the first kind, usually arising as a result of an accident or one-time spill of industrial wastes, are well known (Fontaine, 1966; Mironov, 1972; Aubert, 1973). Fortunately, these areas of intensive pollution are usually located within very limited zones in the sea and the results of such events, even if quite severe, do not extend over broad areas of water. The second group of effects is not so obvious, and has been much less studied. Due to differences in the level of resistance of various species and of various stages of ontogenesis of hydrobionts, a complex chain of biologic reactions and responses arises in the community, the final and most significant manifestation of which is a change in the equilibrium and stability of the community. These changes may be manifested as a decrease in the index of species variety (Bechtel, Copeland, 1970), a disruption in the timing and relationship of processes of production and destruction of organic matter (Kamshilov, 1968), anomalies of the dynamics of dissolved oxygen (Braginskii, 1972), changes in dominant species in the biocenosis (Bellan, Bellan-Santini, 1972) or other ecologic disruptions (Woodwell, 1970).

The non-obvious nature of this type of result, in comparison to acute intoxication (for example, massive fish kills) does not mean that these consequences are any less serious or significant. The situation is more probably the opposite, considering the scale and universality of large-scale pollution, as well as its other aspects, noted above (correlation with distribution of biologic productivity, constancy of levels, etc.); we can assume that large-scale ecologic anomalies are occurring in the ocean. This aspect has not as yet received its deserved attention from researchers, although its importance and urgency for the entire problem of pollution are obvious. In this respect, processes of biologic productivity in the ocean and, particularly, of the formation of organic matter under conditions of chronic pollution of the euphotic zone, should be given particular attention. The problem here is not only related to the fundamental ecologic significance of primary production as the material and energetic basis of life in marine bodies of water, but also the increased vulnerability (sensitivity) of photosynthesis and the community structure of single-celled algae to disruptions in the chemical composition of the environment in which they live. The clearest and best known examples of ecologic anomalies of this type are cases of eutrophication (or, more precisely, hyper-eutrophication) of sea water and, particularly, fresh water, as a result of the entry of large quantities of biogens from the land into the water.

Less known and not so well studied are examples of inhibition of growth, development and photosynthesis of marine phytoplankton as a result of the content of various toxicants or their combinations in sea water. Table 3 presents summarized ecologic-toxicologic information on the effects of toxicants on cultures and natural communities of marine phytoplankton. As we compare the orders of magnitude presented in Table 3 (greater accuracy is impossible, since we are speaking of general features of a complex and dynamic system), it is easy to see that in spite of the great variability, the levels of threshold toxicity of the substances in question for phytoplankton overlap the range of the content of these same substances in the neritic zone, and for some toxicants (petroleum products, polychlorinated biphenyls)--the oceanic zone as well. In other words, the presently existing and repeatedly recorded concentrations of the most common man-made products in sea water are capable of altering the rates of formation of organic matter in the World Ocean.

The extrapolation of experimental data to natural ecosystems which lies at the basis of this conclusion is, naturally, based on certain assumptions. However, if we consider that some of the data in question were obtained under conditions in situ and in long-term experiments, and that there is direct proof of disruptions of the production and structural characteristics of marine phytoplankton in anthropogenically changed environments (Clutter, 1970; Kiryushina et al., 1975; Oradovskii, 1975; Patin, Ibragim, 1975), the idea of large-scale inhibition of photosynthesis, at least in the most polluted regions of the neritic zone of the World Ocean is, in our opinion, well founded. The question of the ecologic results of a large-scale inhibition of photosynthesis in the World Ocean is worthy of special study. For example, a large-scale decrease in primary production by 10%, which hardly seems excessive to us, given today's level of pollution, should result in a corresponding decrease in the rate of production at other trophic levels, right up to the nekton, where these losses would amount to tens of millions of tons, including several millions of tons of commercial fish, each year.

Table 3. Natural, anthropogenic and toxic (for phytoplankton) levels of the content of chemical ingredients in the euphotic layer of the marine environment, μg/l.

Ingredients	Natural levels	Anthropogenic levels Oceanic zone	 Neritic zone	Threshold toxicity level*
Dissolved petroleum products	-	$10^{0}-10^{2}$	$10^{2}-10^{4}$	$10^{1}-10^{3}$
Heavy metals				
Mercury	$10^{-2}-10^{-1}$	$>10^{-2}$	$10^{-1}-10$	$10^{-1}-10$
Lead		$10^{-2}-1$	$10^{-1}-1$	$10^{0}-10^{4}10^{1}-$
10^{3}				
Cadmium	$10^{-2}-10^{-1}$	?	>1	$10^{1}-10^{2}$
Chlorinated hydrocarbons				
Aldrin	-	$<10^{-2}$	?	$10^{-1}-10^{-3}$
Benzylhexachloride	-	$<10^{-2}$	?	$10^{-1}-10$
Polychlorinated biphenyls	-	$10^{-2}-10^{-1}$	$10^{-1}-10$	$10^{-1}-10$
Aliphatic hydrocarbons	-	$10^{-3}-10^{-2}$	?	?
DDT and its metabolites	-	$<10^{-2}$	10	$10^{-1}-10$

*Minimum concentration of toxicants in the environment at which significant (usually 50% inhibition of photosynthesis or of cell division of phytoplankton has been observed.

Among the probable anthropogenic modifications of the normal course of hydrobiologic processes in the ocean, which have never been studied, we must also include such phenomena as disruption of the complex system of external metabolic interactions in communities of marine organisms. The exchange of metabolites among organisms, with the high intensity inherent in it and the biochemical specificity of synthesis and consumption of metabolites, plays an extremely important role as an integrating and regulating factor in marine communities (Khailov, 1971). It is not difficult to imagine that even low concentrations of pollutants foreign for the biotope (for example, dissolved petroleum products) could block various metabolic interactions of the organisms and thereby disrupt the system of biologic communication in communities and, consequently, their structural and production characteristics. The same is probably true as concerns sensory connections of hydrobionts, their ethologic reactions, chemoreceptions and other phenomena, the mechanism of which may be disrupted if small quantities of man-made impurities are present. Due to the complexity and "veiled" nature of such effects, little is known of them, but still, observed facts, such as disruptions in the migrations of fish caused by pollution, indicate that such ecologic anomalies are quite real.

Another group of "critical" situations in marine communities is related to the phenomenon of concentration of toxic microimpurities at the boundary between the water and the atmosphere and between the water and the bottom, which we mentioned earlier, and the influence of toxicants on the most vulnerable organisms and communities of the neuston and benthos. Whereas the reactions of the marine benthos to toxic factors have been rather widely studied, particularly in areas of high pollution (Bellan, Bellan-Santini, 1972) and in acute-toxicity experiments (Stora, 1974), the neuston has as yet fallen outside the sphere of marine ecologic-toxicologic studies, although its vulnerability to the influence of toxic factors is known (Polikarpov, Zaitsev, 1969). This opinion is reinforced by many reports concerning increased sensitivity of the early stages of development of marine organisms, many of which pass through a neustonic phase of life and are subject to severe toxic and even mechanical effects resulting from pollutants located in the biotope of the neuston during this period of their life. For example, even such a common phenomenon as a thin film of oil on the surface of the sea can cause the death of the larvae of physostomous fishes, which it isolates from the atmosphere, preventing filling of the swim bladder with air (Vinogradov, 1972).

There are other ecologic situations and aspects of this problem, for example the accumulation and migration of toxicants through the food chain, the suppression of the reproductive functions of organisms, the additive and synergic effects of toxic factors, the varying resistance of organisms of various systematic groups, etc.

In conclusion, let us emphasize once more the very important, in our opinion, large-scale situation of superimposition of the band of maximum pollution on the band of maximum biologic productivity of the world ocean--the neritic zone of the temperate latitudes of the northern hemisphere. It is in this very area, with its constantly increasing background level of man-made impurities, that the effects and anomalies which we have been discussing arise and propagate throughout the entire ocean. It is here that both national and international efforts should be concentrated for the protection of the marine environment from pollution.

2. Accumulation of Radionuclides by Hydrobionts and Its Results.

(G. G. Polikarpov)

The accumulation of radionuclides, like other substances, by marine organisms is one difference between the processes by which they reach the environment and are removed from the environment. In the extreme case, when removal can be ignored, for example in the building of skeletons, the maximum capability of hydrobionts for accumulation of an element and its radioactive isotopes from the marine environment is revealed, that is, practically all of the element is accumulated. For example, the skeleton of *Acantharia* consists of strontium sulfate; therefore, their spicules contain 6 10^5 times more strontium (and Sr^{90}) than the environment. The shells of mollusks are constructed of calcium carbonate in the process of biologic extraction of calcium from sea water. In addition to the practically permanent store of Sr in the spicules of the *Acantharia* or Ca in the shells of the mollusks, these and other elements are metabolized in their bodies. The higher the rate of excretion, the lower (in the case of the excreting store of the element and its radioisotope) the level of accumulation of the substance in question. When the rates of excretion are similar to the rates of accumulation of an element (radionuclide) is prevented and the result is identical to the result of processes which prevent penetration of the element (radionuclide) through the tissue and membrane barriers.

Of course, during a period of time which is short in comparison to the life cycle of the organism the accumulation is not great, since it involves only the quantity of the corresponding element (radionuclide) and population of its carrier which are present. The maximum possible accumulation in all of the stores, including those which have little or no exchange with the environment, occurs when an element (or radionuclide) is constantly present in the environment throughout the entire life cycle of an organism. If the organism is exposed only to rapidly exchanging supplies of a given element (radionuclide), relatively brief contact of the organism with the element (radionuclide) may be sufficient. This is also correct if the element (radionuclide) is accumulated only by adsorption from solution (in the form of ions, suspensions, on micelles, etc.). Therefore, the accumulation factors must be subdivided into saturated and unsaturated factors.

Values of concentration function.--The many reports which have been published on the accumulation coefficients of the chemical elements whose radionuclides are formed upon nuclear explosions or operation of nuclear enterprises are summarized in Table 4. The range of these coefficients is great: from insignificant (1) to tremendous (10^6). For many elements, a similarity is observed between the values of accumulation coefficients for all trophic levels, while for some a decrease or, conversely, an increase is observed at the level of the predators.

Table 4. Range of coefficients of accumulation of marine organisms at various trophic levels (Bowen et al., 1971; Polikarpov, 1966)

	Producers		First Order Consumers			Higher Order Consumers	
Element	Attached algae	Phytoplankton and sargasses	Copepoda, Pteropoda, Salps, Dolioliids	Benthic mollusks	Euphausiids, Planktonic, Amphipoda, and Shrimp	Fish	Cephalopoda
Ag	100-1000	<100-220	<100	330-20,000	<45-900	-	900-3,000
Cd	11-20	<350-6,000	<80-100,000	100,000-2,000,000	<300-10,000	>10	2,800
Ce	100-3,300	2,000-1,500	-	40-300	-	5-12	-
Co	15-740	75-1,000	<110-10,000	24-260	<70-1,300	28-560	<200-50,000
Cr	100-500	<70-600	15-10,000	60,000-300,000	<55-3,900	3-30	<70
Cs	16-50	16-22	6-15	3-15	-	6-10	-
Fe	1,000-5,000	750-70,000	440-60,000	70,000-300,000	3,000-30,000	400-3,000	1,000-3,000
I	160-7,000	-	-	40-70	-	10	-
Mo	10-200	<3-17	2-175	30-90	<2-14	200	<10
Ma	20-10,000	300-7,000	21-4,000	3,000-60,000	270-1,600	95-100,000	1,000
Ni	50-1,000	25-300	2-1,000	4,000-10,000	17-90	-	30-80
Pb	8,000-10,000	<1,000-3,000,000	3,000-2,000,000	39-5,000	200-60,000	5-10,000	100-200,000
Ru	100-1,200	<200	<10-6,000	1-16	10-2,400	10	<400-2,100
Sr	0.1-90	0.9-54	1-85	50	1.2-10	4-5	0.9-1.2
Ti	200-30,000	600-10,000	28-30,000	-	110-20,000	-	300-3,000
Zn	80-3,000	200-1,300	125-500	1,400-100,000	50	280-20,000	2,500
Zr	200-3,000	<1,000-20,000	360-30,000	8-36	<800-40,000	5	20,000

The values of the concentration function of plankton in relationship to a number of elements are quite great. For example 1 g of plankton ash concentrates in itself a quantity of boron equal to its content in 32 ml of sea water, along with a quantity of aluminum equal to its content in 300 l of sea water.

Plankton also quite actively concentrates P, Cu, Cd, Ti, Cr and other elements. Significant concentration of radionuclides by pelagic crustaceans occurs during the first hours after the beginning of exposure. For example, the Copepoda, during the first three hours, usually accumulate from one third to one half of the quantity of Mn and Co^{60} which they accumulate over the next two days. Our attention is drawn by the nonuniformity of accumulation of radionuclides by different individuals of the same species. Usually, the young members of the species concentrate these elements more rapidly than mature members. This phenomenon has been specially studied from the standpoint of its significance for the formation of absorbed doses of ionizing radiation from the radionuclides accumulated by hydrobionts (Ivanov, Parchevskaya, 1975).

Radioactivity of the environment and its significance in the life of hydrobionts.--A comparison of the absorbed doses of various radionuclides in the tissues of a number of animals of the Sea of Okhotsk and the Bering Sea (herring, seal, whales) shows that the primary contribution is made by K^{40}, with artificial radionuclides (Cs^{137}, Sr^{90}, Y^{90}) playing a secondary role.

A comparison of the doses accumulated in the Sea of Ireland by phytoplankton and zooplankton, mollusks and crustaceans, benthic and pelagic fish, from the natural background, global radioactive fallout and the dumping of radioactive wastes in the vicinity of Windscale has shown that the global fallout usually does not exceed the contribution of the natural background radiation. However, the wastes dumped into the Irish Sea by the Windscale enterprises create a dose level which is higher than the natural background: for phytoplankton by a factor of something over 10, for zooplankton by a factor of over 100, for the benthos and fish--by a factor of up to 100.

Various organisms differ sharply in their sensitivity to ionizing radiation. Most sensitive are certain crustaceans and fish. Beginning with an SR^{90}-Y^{90} concentration of 10^{-9} curies/l or higher, the frequency of nuclear disorders in a number of marine fish increases (Tsytsugina et al., 1973). The sensitivity of the larvae of two species of sea urchins--Pseudocentrotus depresus Anthocidaris crassispina--to the concentration of tritium differs by a factor of 10^4 (Akita, Shiroya, 1970).

Due to experimental difficulties, there has been insufficient material gathered to draw general conclusions in the area of the effects of radioactive pollutants on the populations and ecosystems in the seas and oceans. This is a matter which should be taken up in the near future, considering the rapid rates of growth of nuclear power engineering.

3. Anthropogenic Thermal Effects on the Population of the Sea.

(S. A. Mileikovsky)*

One component of anthropogenic pollution of marine coastal and estuarine waters is so-called "thermal pollution," the dumping of heated water into the sea, after it has passed through the water-cooling systems of electric power plants and industrial enterprises. Evaluating the influence of various components of anthropogenic pollution of sea water on its living resources, Dybern (1974) included thermal pollution in the second most harmful category of "significant pollution factors" of the sea.

Special studies and calculations have shown that as the power of an electric power plant or industrial enterprise increases, the available reserves of fresh water become insufficient to support normal operation of the water-cooling system. Due to this, an increasing number of these enterprises will be placed on the shores of estuaries and bays, utilizing the more abundant supplies of water which they provide. For example, it was calculated for the USA (Picton, 1960) that by 1980, 32% of all thermal electric power plants in the nation would be located near estuaries. This tendency toward placement of electric power plants and industrial enterprises along the sea coast means that the volume of thermal pollution of marine coastal and estuarine waters will increase and its significance as an ecologic factor will grow.

3.1 Amount of Thermal Pollution of Marine Coastal and Estuarine Waters, Temperature of Waters Dumped and Changes in Temperature of Natural Waters which Result

The total amount of thermal pollution of the sea has never been calculated, although some idea of the scale of the phenomenon can be gained on the basis of a number of data. Along the east coast of the USA by late 1968 there were 86 electric power plants burning fossil fuel (coal, oil), dumping their heated water into estuaries, bays and fresh water bodies near the sea (Sorge, 1969). On the west coast of the USA, electric power plants with a total power capacity of 17.2 million kW were dumping their heated waters into the sea, and in California the capacity of these power plants represented 85% of the total electric power generating capacity in the state (North, Adams, 1969). It has been calculated (Mihursky et al., 1970) that in the USA some 4 million m^3 of fresh and sea water are utilized for water cooling of electric power plants and industrial enterprises every minute of every day; the temperature of the water dumped is 5 to 15°C higher than the temperature of the natural waters receiving the heated water.

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*Deceased.

In Japan, nuclear electric power plants alone will consume 130,000 m^3 of sea water permitted for cooling purposes by 1980 (Niva, 1973).

The Hunterstone nuclear power plant (in Scotland) dumps 91,000 m^3 of water with a temperature of water 8-10°C higher than the natural water into the Firth of Clyde each hour. As a result, the surface temperature in the region of this thermal pollution is increased by 3-5°C (Barnett, 1971, 1972).

Usually, the temperature of water dumped by electric power plants and industrial enterprises is 5 to 13°C higher than the temperature of the natural waters, and in some cases it has been heated by as much as 14-24°C.

Regular thermal pollution changes the annual course of temperature of natural waters. For example, at Marchwood on the south coast of England, before construction of the thermal electric power plant in the mid-1950's, the minimum temperature of the surface water (February) was 1-2°C (in 1954, the temperature dropped to -1°C) while the maximum (in August) was 22°C; after the power plant went on stream, the temperature never dropped below 6.5°C in winter and in summer it rose to 26.5-27°C (Raymont, Carrie, 1964).

In Copenhagen Harbor, the water temperature near the area of thermal pollution of one factory reached 6°C even in winter, while in Southhampton Harbor, 400 m from the thermal dump of an electric power plant, it was 3°C higher than the natural temperature, and in the discharge canals of electric power plants in the Patuxent River estuary (Chesapeake Bay) it was 6.3°C higher, and in Biscayne Bay (Florida)--5°C higher than the temperature of the natural water receiving the thermal discharge (Naylor, 1965b; Nauman, Cory, 1969; Thornhaug et al., 1973).

3.2 Influence of Thermal Pollution on the Conditions of Existence of Flora and Fauna

The dumping of heated waters into the sea leads to an increase in the temperature of the natural waters of the region, a decrease in their oxygen content, a decrease in viscosity, a shift of the hydrologic seasons in the surface layers (abnormal lengthening of the hydrologic summer). These changes, in turn, lead to changes in the nature of circulation of water in bays and estuaries, stagnation of water, and increase in the rate of sediment formation and silting, particularly in the summer.

The effect of thermal pollution on the aquatic communities of the estuaries, bays and other marine coastal areas can be quite varied in form, being direct and indirect, ranging from very strong to weak. Heating of natural waters by 4-6°C (and in the summer, sometimes, by only 1°C--Bush et al., 1974) may result in the death of a number of stenothermal species, suppression of the breeding of many species, changes in the specific composition of communities due to replacement of local species with thermophilic intruders, changes in many biologic characteristics of local species--metabolism, shape formation of colonial animals, behavior, nutrition, etc. This heating may lead to a decrease in the intensity of photosynthesis of plants, an increase in oxygen consumption in animals due to intensification of metabolism (which, when the oxygen content of the water is reduced, has a harmful influence on them), an increase in the susceptibility of local species of animals and plants to various toxic substances and pathogenes, possibly causing massive death of species. As a result of the stagnation of water caused by thermal pollution, there may be cases of massive development of algae and, consequently, processes of decay, which have a depressing effect on many species. Thus, thermal pollution disrupts the normal ecologic balance of communities inhabiting the natural waters in the area of the thermal discharge.

For example, in Chesapeake Bay, under the influence of thermal pollution, a population of commercially valuable soft-shell clam, *Mya arenaria*, died and was replaced by the small, noncommercial species *Gemma gemma*, which has a higher level of heat tolerance (Kennedy, Milhursky, 1971). In the region of Cape Cod, thermal pollution, on the other hand, stabilized the population of the mussel *Mytilus edulis*, by depressing the feeding of its primary enemies--the sea star *Asterias forbesi*, the dog-whelk *Thais lapillus* and the crab *Carcinus maenas* (Pearce, 1969).

The decrease in the population of the bivalve *Mulinia lateralis* in the waters of the Atlantic coast of the USA, resulting from thermal pollution, has significantly harmed water birds, for which it was a diet staple (Kennedy et al., 1974).

3.3 Influence of Thermal Pollution on the Distribution of Flora and Fauna

Benthos.--Examples of the influence of thermal pollution on the benthos have been accumulated for some time, primarily for various areas along the Atlantic coast of the USA. In the estuary of the Patuxent River and a number of other areas of the Chesapeake Bay, thermal discharges have greatly decreased the areas of the plant *Ruppia maritima*, while increasing the biomass, population and density of epifauna (Anderson, 1969; Cory, Nauman, 1969; Nauman, Cory, 1969). In Biscayne Bay, thermal pollution caused disease, then death of blooming plants and macrophytes and changes in the composition of the zoobenthos (Roessler, zieman, 1969; Wood, Zieman, 1969; Thornhaug et al., 1973). In other areas of the Florida coast, thermal pollution has been found to influence the distribution and migration of the commercial blue crab *Callinectes sapidus* (Nugent, 1970; Leffler, 1972).

In one bay along the California coast, in a heated area, the species variety of bivalve mollusks increased, while in other bays the composition of benthic communities changed (North, 1968).

Thermal pollution in Hawaii caused the death of corals in the region of the thermal discharge and the transformation of the reef to dead limestone covered with sand (Jokiel, Coles, 1974). Changes in the benthos of the Baltic Sea coastal area, observed by Swedish investigators in an area of thermal discharge from a 3 million kW nuclear power plant were similar to those observed in natural waters during the hot summer of 1968, when the water temperature was 9-10°C higher than usual for a period of 3 weeks (Ankar, Jansson, 1973). There are other examples of the influence of thermal pollution on the distribution of the benthos.

Plankton.--Data on the influence of thermal pollution on the distribution and composition of plankton are as yet sparse. For example, it has been shown that in the vicinity of Southhampton (Pannel et al., 1962; Raymont, 1964; Raymont, Carrie, 1964), thermal pollution has caused a gradual increase in the population of the warm-water copepod Acartia tonsa, and in the summer plankton the larvae of the warm-water cirripedian Elminius modestus have become numerically dominant, quite unusual for northern European waters. On the other hand, in the Patuxent River estuary, the thermal discharge did not cause changes in seasonal parameters of the distribution of Acartia tonsa and Eurytemora affinis (Heinle, 1969b). Similarly, off the coast of Japan, the thermal discharge of nuclear power plants in most cases did not result in a decrease in the population of zooplankton, and in many cases there was even an increase in its population (Niva, 1973).

Fish.--Depending on the thermopathy, various species of fish are attracted to or repelled by regions of thermal discharge. In western European waters, for example, cases of winter concentration of a number of fish in regions of thermal discharge have been observed.

3.4 Passage of Pelagic Fish through the Pipes of Water Cooling Systems of Nuclear Power plants and Industrial Enterprises

One very important form of thermal pollution is its effect on pelagic animals as they pass through the pipes of the cooling systems of power plants and industrial enterprises. Passage through the pipes has different effects on different organisms, and this phenomenon itself may lead to different ecologic results. In the Patuxent River estuary, passage of phytoplankton through the pipes of the cooling system of the power plant in the summer inhibits photosynthesis, while in the winter it cancels the stimulating effect of the increased temperature of the water on photosynthesis; as a result, it may lead to a decrease in the photosynthetic activity of the phytoplankton by a factor of 10 (Morgan, 1969). Inhibition or stimulation of the photosynthesis of phytoplankton as it passes through the cooling pipes of electric power plants have also been observed in the York River estuary in Virginia (Warinner, Brehmer, 1966).

Many planktonic copepods die, primarily as a result of mechanical damage, as they pass through the cooling system of the power plant in the Patuxent River estuary, and 90% of zooplankton eggs lose their capacity to hatch (Heinle, 1969a); in the water cooling pipes of a power plant near New York, from 70 to almost 100% of the copepods died (Suchanek, Grossman, 1971; Carpenter et al., 1974).

It has been shown for Acartia tonsa (Reeve, Cosper, 1970) that if it is held at temperatures characteristic of the thermal discharge waters dumped into Biscayne Bay, the mortality rate is twice as high in winter as in summer. However, the larvae of bivalve mollusks can pass through the water cooling pipes of power plants without harm and settle, forming normal populations in thermal discharge regions (Adams, 1969; Barnett, 1972).

It has been thought that the juveniles of various fish can pass through the water cooling pipes of power plants without harm (Kerr, 1953; Markowski, 1959). New studies (Marcy, 1971), however, have shown that the mortality of fry is very high in such situations.

Thus, water cooling systems of power plants and industrial enterprises located along sea coasts and estuaries have a significant influence on the population and reproduction of plankton, benthos and nekton.

3.5 Change in the Specific Composition on Communities in Regions of Thermal Discharge

The change in the specific composition in regions of thermal discharge has been most thoroughly studied for coastal benthic communities. The barnacle Balanus amphitrite, entering western European waters from the subtropics and tropics, has formed stable populations in regions of thermal discharge along the coasts of southern England, Wales and Holland (Stubbings, Houghton, 1964; Naylor, 1965a; Borghouts-Biersteker, 1969). Near Southhampton, in the area of thermal discharge from the Marchwood electric power plant, a stable, self-reproducing population of the bivalve mollusk Mercenaria mercenaria has formed--an intruder from the northwest Atlantic (Ansell, 1969). In Swansea Harbor (Wales), due to the heating of the water by the thermal discharge of a power plant, new warm-water species of corals, polychaetes, bryozoans, camptozoans, cirripedians, isopods and fish have appeared, some from subtropical and tropical waters, some from the warm-temperate regions located to the south; at the same time, a number of local species have disappeared from the benthos at the point where the warm waters are discharged (Naylor, 1965a).

A similar picture has been observed for the coastal benthos and nekton in many other regions damaged by thermal pollution.

3.6 Influence of Thermal Discharge of the Biology of Organisms

The influence of heating of waters on the biology of organisms may be either negative or positive. Thermal pollution may influence the intensity of photosynthesis of phytoplankton, accelerate the occurrence of biochemical processes in organisms and increase their susceptibility to disease. Heating of water influences the intensity of respiration, the stability and integrity of leaves and stolons of littoral and sublittoral blooming plants and macrophytes. In the estuaries of Florida, the turtle grass Thalassia testudinum has lost some of its leaves under the influence of thermal discharge, but retained healthy stolons; however, in cases of severe and permanent heating, the accumulation of heat by sediment has resulted in loss of strength by the stolons, which are then broken (Wood, Zieman, 1969).

Thermal pollution changes the seasonality and intensity of migration of a number of benthic invertebrates, the feeding rate (which sometimes decreases, sometimes increases), the growth rate (which increases), the maximum size and size upon achievement of sexual maturity, shell thickness, volume of accumulation of various chemical elements in the body tissues (for example, oysters accumulate an excess of copper, which has a depressing effect on them).

Thermal pollution has a severe effect on breeding, larval development and reproduction of organisms in the sea and estuaries, particularly benthic invertebrates in the vicinity of the thermal discharge (Davis, 1972; Verwey, 1973; Mileikovsky, 1976). The most usual result of this effect is earlier beginning and longer duration of the periods of breeding and spawning. This picture was observed for benthic invertebrates in regions of thermal discharge of electric power plants along the coasts of England, Wales, Scotland and the USA (Pannell et al., 1962, Naylor, 1965a, b; Adams, 1969; Barnett, Hardy, 1969; Barnett, 1971, 1972). Induction of reproduction out of season has also been noted for marine plants (Wood, Zieman, 1969). The earlier beginning and longer duration of the reproductive and spawning season usually give the species involved certain advantages and increase their competitiveness, although at times the earlier beginning of spawning simply means that some of the fry die because they are hatched too early (Barnett, Hardy, 1969).

In temperate and cold waters, thermal pollution creates favorable conditions for the reproduction of various intruders from warmer waters (Ansell, 1963; Raymont, Carrie, 1964; Stubbings, Houghton, 1964; Naylor, 1965a, b; Adams, 1969).

Under the influence of the heating caused by thermal discharge, the duration and time of settlement of pelagic larvae of some forms of benthic invertebrates change (becoming longer for most species), the nature of succession changes, and the settling rate increases. All of this results in the formation of more abundant epifauna in regions of thermal discharges, and sometimes of infauna as well, than in normal areas.

3.7 Degree of Harm of Thermal Pollution of Marine Coastal and Estuarine Waters

The question arises: what is the specific harm of thermal pollution at its present level of intensity? The data which have been gathered indicate that in most cases, the harmful effect is not very strong, and is manifested in small regions in the immediate vicinity of the discharge of heated water. Based on the fact that the effect of the thermal discharge of the Hunterstone nuclear power plant (Scotland) on the fauna of the Firth of Clyde is quite limited, it has been assumed that in the temperate latitudes, thermal pollution, at today's scale, will have no harmful influence on the marine biota. However, should the volume of thermal pollution increase in the future, unexpected ecologic effects may occur (Barnett, 1971).

Since the volume of thermal discharge into marine coastal and estuarine waters continually increases, the question of the development of methods of checking the effects of thermal pollution takes on particular significance. The protective measures which have been suggested are few and sometimes contradictory. All authors agree that the most important thing is to provide the most rapid possible mixing of the heated discharge water and natural water, to cool the warmer water to the natural level as quickly as possible. To do this, it has been suggested that electric power plants and manufacturing plants either be constructed along open areas of the sea coast with surf, and the thermal water be discharged at some depth (Glooschenko, Glooschenko, 1969), or that heated water be discharged into special mixers (Verwey, 1974) or into the open sea (Barnett, 1972). However, it has been noted that estuarine biota have been adapted by evolution to great fluctuations in environmental factors, including temperature, much better than the biota of open sea coasts (Cairns, 1969; Brungs, 1970; Patric, 1972).

We must not forget the possibility of using thermal discharge to meet the economic needs of man. Heated water can be used to develop the farming of commercial species of algae, invertebrates and fish in regions of thermal discharge. The first experiments along this line have already been undertaken in several countries. The possibility has also been reported of increasing the effectiveness of reproduction of fish and invertebrates in cold-water regions by the use of heated water (Davis, 1972), as well as the use of heated water to control fouling (Naylor, 1965b).

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